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JOURNAL OF ANATOMY

SOME OBSERVATIONS ON MYELINATION IN THE HUMAN CENTRAL NERVOUS SYSTEM

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The first appearance of the myelin sheath in fibres of the central nervous system is a subject that has attracted attention for many years, more particularly since Flechsig (1) originated the view that the degree of myelination might be correlated with functional capacity. His original theory stated that myelination was found in projection paths always before association paths, and in peripheral before central paths, and in sensory before motor ones. These statements were not fully confirmed by Monakow, Vogt, Westphal and others (2), and Flechsig subsequently modified his theory but still maintained that with respect to any one projection centre the fibres always myelinated in the same order, namely, first the sensory, then the efferent, and then the association fibres. On the other hand, Vogt (3) states that myelination depends on the number and size of the fibres developed in the path, and is not correlated with the function of the fibres.

Flechsig's theory has been found to apply in kittens by Tilney and Casamajor (4), who investigated the development of various somatic motor reactions from birth up to 4½ weeks, and attempted to correlate these reactions with the myelination found at various ages.

It cannot, however, be a rule of general application that myelination is a criterion of functional activity of the conducting paths. Gonzalez (5) has shown that in white rats myelination does not begin until after birth, and yet in a 19-day foetus definite reflexes are possible with an inhibitory control from higher centres. Further work confirming Gonzalez' view has recently been published by Wenderowic (6).

Quite apart from the functional significance of the appearance of the myelin sheath, the investigation of the myelination present at various stages of development has been used as a means of tracing the course of nerve paths between higher centres and the periphery. No systematic account of this development has yet been published for the human foetus, and the present paper is an attempt to confirm and extend observations of other workers. The collection of suitable material is a difficult matter, and it is realised that the series on which the paper is based is as yet in some ways incomplete, but it is

hoped to continue the investigation as material becomes available. Whilst this paper was in course of preparation an account of the myelination present in a 7th month human foetus has been published by Langworthy (7): his observations are in agreement with ours with respect to those fibre groups that are discussed both in his paper and in ours, but he investigated also the myelination in the cerebellum which we have not done.

The origin and formation of myelin has been described by Cornwall (8), Schultze (9), Berberich (10), and others: Cajal (11) regards its formation as due to the activity of the axis cylinder, beginning centrally and extending peripherally, and gradually increasing in thickness.

METHOD

The material on which this paper is based includes serial sections of brain stem and spinal cord from thirteen foetuses varying in age from 14 weeks to full time, and also from three infants under 1 year old. The ages of the foetuses were determined by taking into account the maternal history, together with the data obtained from careful observation and dissection of the foetus. The foetal specimens include one each of the following ages: 14 weeks, 16 weeks, 20 weeks, 22–24 weeks, 23–25 weeks, 24–26 weeks, 26–28 weeks, 28 weeks (lived 19 days, see below), 36 weeks. In addition there were four full-time specimens, and three infants aged 3, 8 and 9 months respectively. The foetuses dissected varied only within physiological limits, that is, were apparently "normal." The tissues have been obtained as fresh as possible, carefully dissected out, and fixed first in formalin and subsequently in Muller's fluid. Further treatment involved staining by the Weigert-Pal method, the sections being cut in celloidin and mounted serially. In addition to these serial sections nine other specimens of various ages have been investigated by the Bielschowsky and Ranson methods.

GENERAL OBSERVATIONS

The appearance of myelin as shown by the typical staining reaction of the Weigert-Pal method is preceded by some change in the nerve fibres that gives rise to a very characteristic brownish grey coloration in sections so stained. This may be termed the "pre-myelin" stage: it is of short duration, and is followed by the well-known dark blue staining reaction.

In tracing out the course of the various fibres we have been able to confirm the observation (11) that myelination proceeds centrifugally, and also that in some cases at least a nerve path of several neurones myelinates in neurones in the order of conduction of the impulse. An example of this is to be found in one of the sensory paths: the fibres of the column of Burdach begin to myelinate at about 14 weeks' development; the second neurone of this path may be the medial fillet which begins to myelinate at about 24 weeks, or the external arcuate fibres which are not myelinated until nearly full time. The thickness of the myelin sheath increases gradually from its first appearance as a thin

covering to the axis cylinder: it has been suggested that this gradual increase may be correlated with the increase of growth in the size of the axis cylinder itself.

In the course of this investigation it was found that one specimen did not fall into line with the remainder of the series. The history was one of 28 weeks' gestation, and in the other specimens of this stage of development no myelination had ever been found in the pyramidal fibres, or in the pons fibres, or in the optic tract: in this particular specimen myelination was present in these three groups of fibres to the extent corresponding to the conditions found about the time of birth (40 weeks' gestation). Further inquiry into the history revealed the fact that the child, although born at 28 weeks' gestation, had lived for nearly 3 weeks.

In the following account the main afferent and efferent paths are first considered, then the chief connecting paths, and lastly the cranial nerves. The myelination of the various fibre groups in the thalamic and subthalamic regions is barely touched upon, as it is hoped later to make a further and detailed investigation of this part of the brain.

(A) MAIN AFFERENT PATHS

(1) *Posterior root fibres*

By 14 weeks' development a very few of the posterior root fibres are finely myelinated: the number of fibres myelinated and the thickness of the sheath increase steadily but more obviously after 24 weeks (fig. 1).

(2) *Posterior column fibres*

Fine myelination is present in a few fibres of the column of Burdach near the base of the posterior columns by 14 weeks: by 22–24 weeks the number of fibres myelinated has increased considerably, but the sheath is still extremely fine. From the 24th week onward the degree of myelination becomes markedly heavier, and at birth these fibres stand out in the sections as among the most intensely stained.

Fibres in the column of Goll acquire their myelin sheath later, the earliest seen being by 23 weeks: the degree of myelination gradually increases, but even after birth the fibres do not appear so deeply stained as those in the column of Burdach. As is well known the fibres of Goll's column are smaller in cross-section even in the adult than those of Burdach's column, and therefore this tract appears less darkly stained of the two (figs. 1 and 3).

The nuclei gracilis and cuneatus are clearly differentiated by 14 weeks, but myelination of the second neurone on this path (the medial fillet) does not appear until about the 24th week of development: this myelination is at first very fine, but is present throughout the whole path up to the thalamus. The staining reaction of the medial fillet increases quickly with age, but from 26 weeks until about 8 months after birth definite non-myelinated bundles,

circular in cross-section, can be very clearly seen scattered amongst the myelinated fibres (fig. 11). These bundles can be traced from the origin of the fillet in the medulla up as far as the level of the inferior corpora quadrigemina, and are some of the "aberrant fibres of the pyramidal path" (see below): they cannot be the second neurone on the sensory path of the 9th and 10th cranial nerves that run in the fillet, as these fibres are beginning to myelinate by 14 weeks.

The cerebellar connection from the nucleus gracilis and nucleus cuneatus (the external arcuate fibres) is not myelinated at 36 weeks' development, but the fibres give a faint but definite staining reaction at full time.

(3) *Direct cerebellar tract*

A few very finely myelinated fibres are found at 16 weeks' development: the myelination increases slowly until about 28 weeks, when the stained sections show that it is considerable in amount. At birth this tract stands out in sections as particularly heavily stained (fig. 2).

The fibres are myelinated throughout their course through the restiform body to the cerebellum.

(4) *Gowers' (antero-lateral ascending) tract*

By the 14th week of foetal life a very little myelination is seen in the antero-lateral region of the spinal cord, and it is difficult to distinguish between ascending and descending fibres. After the 28th week myelination is more marked, but even at full time the fibre sheaths are not so thick as in the direct cerebellar tract. Fine fibres crossing in the anterior commissure are myelinated at the 14th week: they belong probably to the spinothalamic and spinotectal groups. In the young specimens (14–24 weeks' development) these crossing fibres are more abundant in the cervical region than lower down the cord (fig. 1).

(B) MAIN EFFERENT PATHS

(1) *Pyramidal tracts*

Some fine myelination is first seen at about 36 weeks' development, particularly at the higher levels of crusta and pons. At full time the myelination is still very scanty, being more marked in the brain stem and in the cervical region of the spinal cord than lower down. The "pre-myelin" stage can be well seen in most of the fibres. Even at 9 months after birth the myelination is still very incomplete, and the sheath comparatively thin.

The "aberrant fibres of the pyramidal path" (Dejerine (12)) that run in the medial fillet can be detected as definite bundles (see above) from 26 weeks' development onwards (fig. 11): they can be traced as unstained circular areas in cross-sections of the brain stem from the level of the lower border of the crura cerebri down to the lower border of the olives, where they appear to join the main pyramidal path. These fibres give the "pre-myelin" staining reaction by

8 months after birth, and by 9 months they are definitely myelinated although the sheath is thin.

Other "aberrant pyramidal fibres" (also described by Dejerine(12) and referred to in the chart as X fibres), can be seen lying in the lateral part of the substantia nigra, just posterior to the crusta: at lower levels these fibres become more anterior, and join on to the main pyramidal path in the pons. This group of aberrant fibres is not myelinated at birth, but 3 months later shows a very heavy degree of staining. They are frequently shown in diagrams of cross-sections, but are not usually named as part of the pyramidal system.

(2) *Rubrospinal tract*

A few fibres show fine myelination by 36 weeks' development, the extent of myelination increasing gradually as in the pyramidal tracts.

(3) *Antero-lateral descending tract*

It is difficult to distinguish between antero-lateral ascending and descending fibres, but the myelination in this position in the cord gradually increases from 14 weeks' development onwards. In a 28-weeks' foetus the olivo-spinal tract can be distinguished in section as a definitely non-myelinated triangular area, and even at 8 months after birth this tract is very incompletely myelinated (fig. 2).

As the fountain decussation of Meynert (tecto-spinal tract) (fig. 13) is finely myelinated by the 24–26th week it is probable that some of these fibres are also myelinated about this time in the spinal cord.

(4) *Anterior root fibres*

A few fibres are already myelinated in a 14-week foetus, the myelination being somewhat in advance of that of the posterior root fibres. After this date myelination increases rapidly, and is very soon a marked feature of all the preparations (fig. 1).

(C) CONNECTING PATHS

(1) *Ground bundles of the spinal cord*

The anterior ground bundle is the first to myelinate, giving a definite staining reaction by 14–16 weeks' development. The lateral ground bundle begins to myelinate about 22–24 weeks, and the posterior ground bundle about a fortnight later (26–28 weeks) (fig. 1).

(2) *Connecting fibres in the grey matter of the cord*

Fine myelinated connecting fibres can be seen by 22 weeks' development, passing between the postero-lateral region of the grey matter and the anterior horn cells. These fibres are not myelinated by 16 weeks, and the number myelinated and the thickness of the sheath increase rapidly.

(3) *Lissauer's tract*

This group of fibres myelinates late: the process was seen to be just beginning by 36 weeks' development, but myelination was not constantly found even at full time (fig. 3).

(4) *Comma tract*

The fibres of this tract are not myelinated before those of the posterior columns: in specimens that gave a staining reaction throughout the columns of Goll and Burdach, the comma tract was not identified.

(5) *Olive and cerebellum connections*

Fibres connecting the olives and the cerebellum begin to myelinate by 22 weeks: after this myelination proceeds rapidly.

(6) *Medial (or posterior) longitudinal bundle*

By 14 weeks' development a few of these fibres show fine myelination throughout the entire distribution of the tract from medulla up to mid-brain, and already at this stage there is a myelinated connection between the bundle and the myelinated posterior commissure (figs. 5 and 11).

(7) *Dorsal longitudinal bundle (of Schütz)*

These fibres begin to myelinate at full time.

(8) *Pons fibres*

A very few fibres are faintly myelinated by 36 weeks' development, but even at birth the myelination is very scanty (fig. 7). By 8 months after birth, however, the staining reaction is well marked.

(9) *Brachia conjunctiva*

Myelination begins at about the 26th week of development, and appears to involve all the fibres: it is not possible to distinguish between the afferent and efferent groups.

(10) *Fasciculus retroflexus of Meynert*

This bundle (fig. 10) can be distinguished as a collection of non-myelinated fibres in a 14-week foetus: by 22 weeks the bundle is still non-myelinated, but by 24 weeks the myelination is quite distinct in the peripheral fibres. This partial myelination persists for some time, but by 36 weeks the whole bundle is well myelinated and can be traced to the ganglion habenulae.

(11) *Cortico-pontine cerebellar tracts*

Myelination of these paths is comparatively late, being very slight indeed at birth. Nine months later myelination is more advanced, but even at that date in the stained sections through the crusta the central pyramidal fibres appear much darker than do the fibres of these groups. The sections show also that the fronto-pontine path is less heavily myelinated than the temporal and occipital fibres at this date ($\frac{9}{12}$ year) (fig. 12).

(12) *Fornix*

The fornix begins to myelinate about 8 months after birth.

(13) *Ansa lenticularis fibres*

There are various groups of fibres that pass across the posterior limb of the internal capsule: some of these begin to myelinate early, before the pyramidal fibres that pass through this region, and are consequently well seen in such specimens (fig. 9). Dejerine(13) distinguishes "radiations strio-luysiennes," which pass from the striate body to the nucleus subthalamicus and then spread out fanwise. These fibres show a "pre-myelin" staining by 24–26 weeks' development, and a definite myelin reaction by 26–28 weeks. The "strio-thalamic" fibres lie more laterally than the above in the internal capsule, and they myelinate later, being first seen at 36 weeks.

(14) *The bundle of Vicq d'Azyr*

This group of fibres is not myelinated at birth, but can be seen in the sections as a definite group of unstained fibres. By 3 months after birth the tract is well myelinated.

(15) *Meynert's commissure*

This band of fibres passes dorsal to the optic chiasma and connects the two lenticular nuclei (Dejerine(14)), and is said by Riese(15) to be the first of the hypothalamic commissures to myelinate. In the 36-weeks' foetus these fibres were already myelinated, and in one specimen of 28 weeks some finely myelinated fibres were seen which were thought to belong to this commissure although not positively identified.

(16) *Olfactory nerve*

The myelination of these fibres was not investigated.

(17) *Optic tract*

By 36 weeks' development a few of the optic fibres are myelinated, but the myelination continues to be inconstant and slight up to full time. At full time the connections with the external geniculate bodies and with the optic thalamus are myelinated. In the 28-week foetus that survived for nearly 3 weeks after birth the optic fibres were beginning to myelinate. (For connection with geniculate bodies see fig. 12.)

(D) CRANIAL NERVES

Nearly all the cranial nerves acquire a myelin sheath early: by 14 weeks' development some myelinated fibres can be detected in all these nerves (within the brain stem) except in the sensory part of 5 and in the cochlear part of 8. By 24 weeks all the cranial nerves contain myelinated fibres, the motor nerves appearing particularly heavily stained.

Nerve 12

The nucleus (fig. 5) is well differentiated by 14 weeks, the cells being of the large multipolar type and extending throughout the whole of the lower

and middle part of the medulla. The myelination is at first fine, but by 26 weeks is extremely heavy, the stained fibres standing out very remarkably in sections through this region.

Nerve 11

The medullary nucleus is differentiated and the fibres finely myelinated by 14 weeks' development. The spinal accessory fibres arising from the cord are myelinated by 26 weeks and possibly before: it is easy to miss these fibres unless complete serial sections are available.

Nerves 10 *and* 9

The nuclei are differentiated and fine myelination is present in the fibres by 14 weeks' development. Of the various nuclei the nucleus solitarius (fig. 4) can be the most readily associated with the myelinated fibres in the younger specimens.

Nerve 8

(*a*) *Vestibular branch.* A few myelinated fibres are present by 14 weeks' development, but it is not possible to be certain with which of the three nuclei they are connected. The nucleus of Roller's bundle (descending branch) can be made out with some myelinated fibres. By 26 weeks the myelination of the vestibular fibres is general.

(*b*) *Cochlear branch* (fig. 7). The fibres belonging to this nerve are definitely not myelinated by 14 weeks, but by 24 weeks many of the cochlear fibres have acquired a fine myelin sheath: they can be traced to their nuclei. The next neurone (striae acousticae and trapezium fibres) is also myelinated, and the myelination can be traced up in the lateral fillet to the inferior corpora quadrigemina and internal geniculate body. The connection with the superior olive is also myelinated by this date (fig. 6).

Nerve 7

Both efferent and afferent parts of the deep connections are myelinated by 14 weeks, although the sheath is thin and not present on all the fibres.

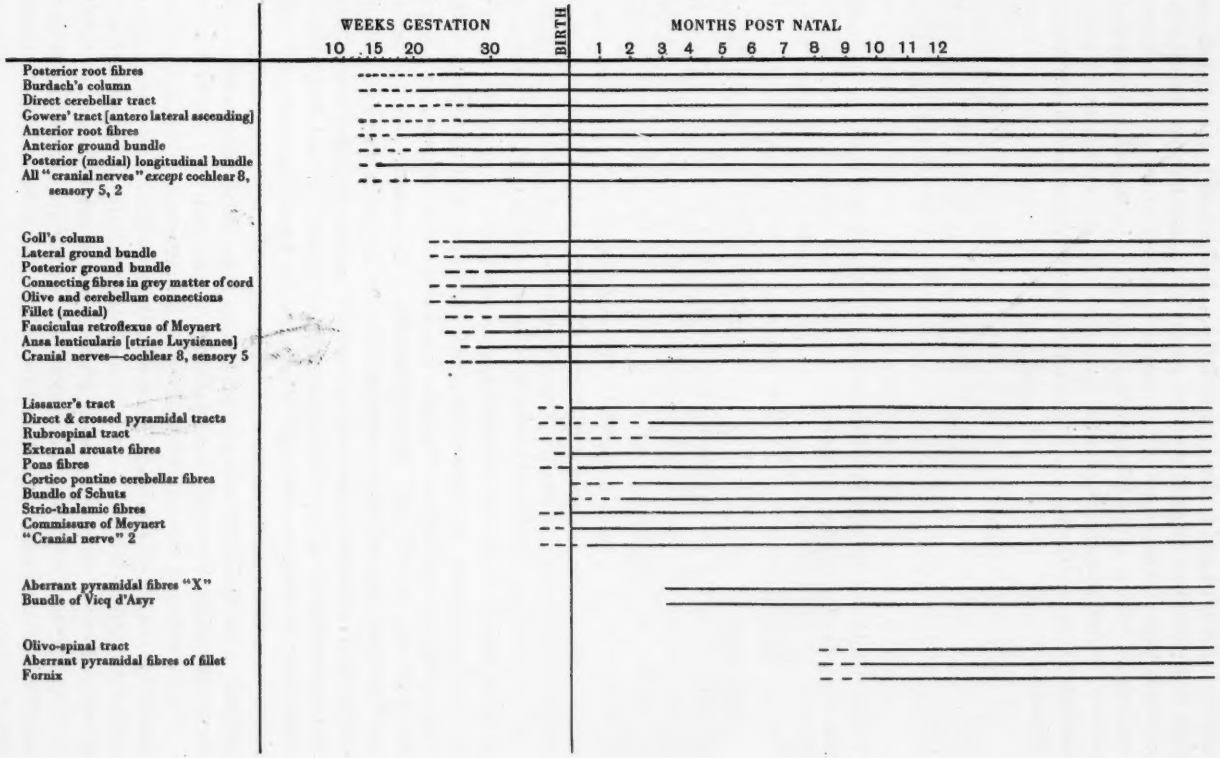
Nerve 6

The nucleus of large multipolar cells is well differentiated by 14 weeks, and some of the emerging fibres are already faintly myelinated. In the older specimens these fibres stand out in the stained sections as having thick myelin sheaths, similar to those of the 12th and 3rd nerves (fig. 7).

Nerve 5

A few myelinated fibres are found arising from the motor nucleus by 14 weeks, but at this time the sensory fibres are still unmyelinated although the sensory nuclei are differentiated. By 22–24 weeks the sensory fibres are myelinating, and the spinal root in connection with the substantia gelatinosa of Rolando contains finely myelinated fibres in the medulla. By 24 weeks the decussating sensory fibres arising from the main sensory nucleus are well myelinated.

TABLE OF DATES OF MYELINATION OF IMPORTANT FIBRE GROUPS



The mesencephalic root (figs. 10 and 11) of this nerve is beginning to myelinate by 14 weeks, and is closely associated in position with the peculiar large cells that extend up beyond the level of the 3rd nerve nucleus (fig. 8). These cells are usually spoken of as the mesencephalic nucleus of the 5th nerve, and are of several types (Sheinin (16)). They give rise to fibres whose precise nature has been much disputed: they may be afferent or efferent, or possibly comprise both centripetal and centrifugal fibres of the autonomic system (see Winkler (17)).

Nerve 4

In the 14-week foetus the fibres of this nerve are just beginning to myelinate. At a slightly later stage myelinated fibres can be easily traced passing from the nucleus of this nerve to enter the posterior longitudinal bundle.

Nerve 8

Myelination is present in a few fibres at 14 weeks, and by 26 weeks most of the fibres are heavily myelinated.

DISCUSSION

The dates of myelination of the important groups of fibres have been summarised in the accompanying chart. It will be seen that there are four definite periods (between 12 weeks' gestation and a year after birth) at which the myelination process appears to receive an impetus. These periods are as follows:

(i) About 14 weeks' gestation.
(ii) 22–24 weeks' gestation.
(iii) Just before full time.
(iv) About 8 months after birth.

In addition, in the tracts that begin to myelinate at about 14 weeks the process is markedly accelerated at about 24 weeks. In this connection it is interesting to note that the "quickening movements" of the foetus are felt about the 5th month, that the weight ratio of the brain remains practically constant from the 24th week onwards (18), that the brain grows most rapidly during the second half of pregnancy (19), and that the majority of the fissures and lobes of the brain are differentiated between the 24th and 28th weeks (19). There may also be some correlation between the marked increase of myelination at this time and the appearance of lipoid in the suprarenal cortex of the foetus (20): the lipoid first appears in traces by 22 weeks' development, and then increases rapidly during the later months of foetal life.

On referring to the chart it will be seen that myelination occurs first in sensory paths, together with the motor cranial and spinal nerve roots, and the medial longitudinal bundle. It is remarkable that the sensory fibres of the trigeminal nerve and the cochlear fibres of the auditory nerve are later in myelinating than any other nerve roots. Of the association paths, the medial longitudinal bundle and the anterior ground bundle of the cord are the earliest to myelinate.

Myelination in the column of Goll is considerably later than that in the column of Burdach. The significance to be attached to the acquisition of the myelin sheath is a debated point, and so it is difficult to explain this delay. Since the rate of growth of the hinder parts of the body lags behind that of the remainder, it is tentatively suggested that there may be some relationship between the rate of growth and the myelination of afferent fibres.

By 28 weeks' development, at which stage the foetus is viable, all the important sensory paths are myelinated, with the exception of such connecting paths as Lissauer's bundle in the spinal cord, and the external arcuate fibres from the nuclei gracilis and cuneatus to the cerebellum. At this age, the long motor paths are not myelinated, but as the association paths in both brain stem and spinal cord and also the motor nerves are all myelinated the nervous activities must be purely reflex, with no central control of cord function.

At birth the long motor paths are beginning to myelinate: the whole of the cortico-pontine-cerebellar path is also myelinating, providing the path for cerebral control of cerebellar responses. In addition, the external arcuate fibres are myelinating, also the bundle of Schütz and Lissauer's tract. Thus all the important connecting paths are myelinated at birth.

The tracts that are not even beginning to myelinate at this time are the olivo-spinal tract and the aberrant pyramidal fibres: of these the aberrant pyramidal fibres X myelinate about 3 months after birth, and the other two groups begin to myelinate together at about 8 months. These aberrant fibres of the pyramidal path are usually missed in stained sections in which both fillet and pyramidal fibres are fully myelinated, although they can be picked out by the small size of their fibres: in this series they show extremely well, because they do not myelinate until so very much later than the fillet fibres. Dejerine (12) has traced their course in Marchi stained preparations of a case of pyramidal degeneration, and our series confirms his description.

It is interesting to note that the late date of myelination of two of the descending paths—namely the olivo-spinal tract (an efferent path from the cerebellum) and the aberrant pyramidal fibres in the fillet (an efferent path from the motor cerebral cortex)—corresponds to the time at which the baby begins to maintain its equilibrium and to perform purposive, co-ordinate movements such as crawling and standing. The baby can carry out certain co-ordinate movements at a considerably earlier date, but since these particular activities become possible at about the same time as the olivo-spinal and aberrant pyramidal fibres myelinate, these may be the special nerve paths concerned, assuming that there is some relation between myelination and function.

At the beginning of this paper it was mentioned that one of the specimens was obtained from a child born prematurely at 7 months and surviving for nearly 3 weeks, and that in this case the myelination found corresponded in certain respects to that of a full-time foetus. This acceleration of the myelination process may be associated with and due to the premature assumption of post-natal conditions, although it is not possible to make out a definite corre-

lation from one case: if this is so, it would lend further support to the view that myelination and functional activity are related.

SUMMARY

1. In the course of human development there are four stages at which the process of myelination receives an impetus:

(i) About 14 weeks' gestation.
(ii) About 22–24 weeks' gestation.
(iii) Just before full time.
(iv) About 8 months after birth.

2. Of these periods the second (22–24 weeks) is the one at which the myelination process is most active.

3. Dates of myelination are given for the more important of the fibre paths, and for the cranial nerves.

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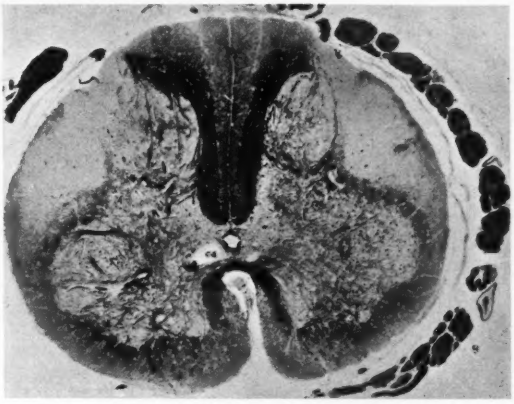

Fig. 1

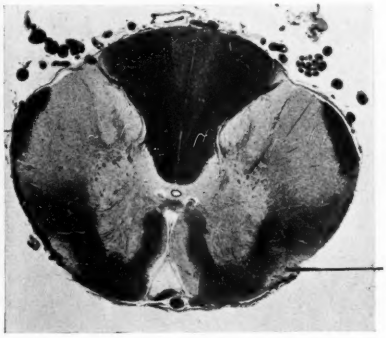

Fig. 2

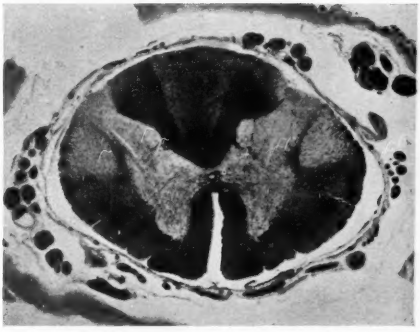

Fig. 3

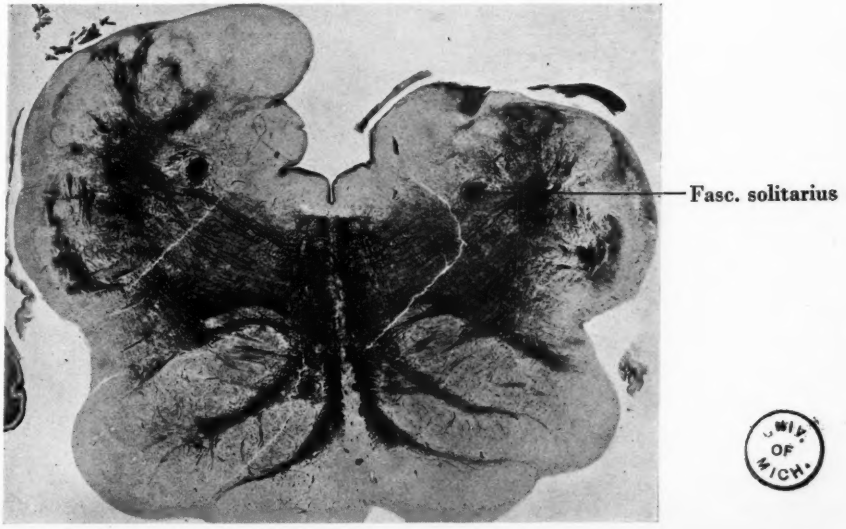

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Fig. 5

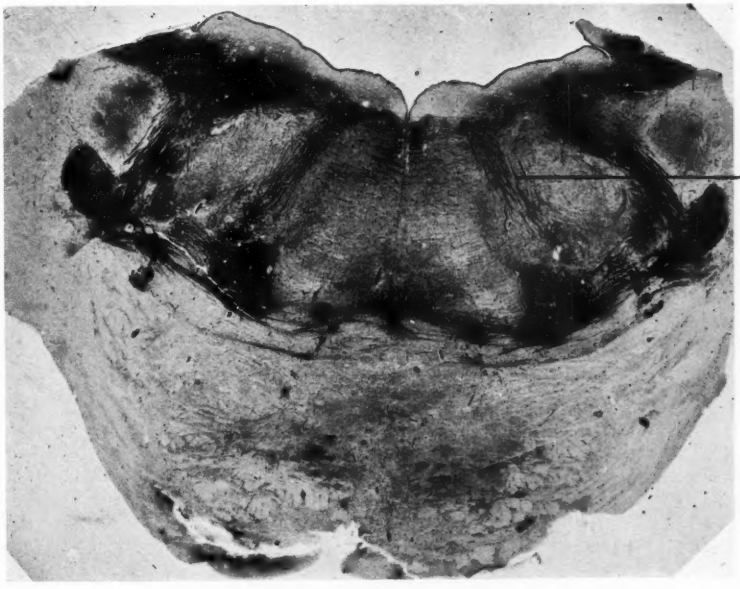

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Fig. 6

Fig. 7

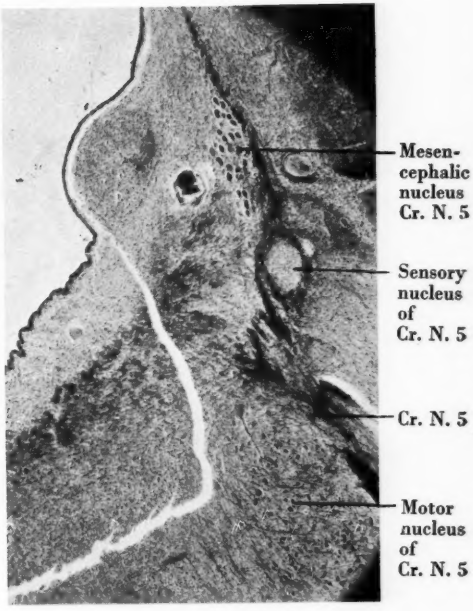

Fig. 8

Fig 9

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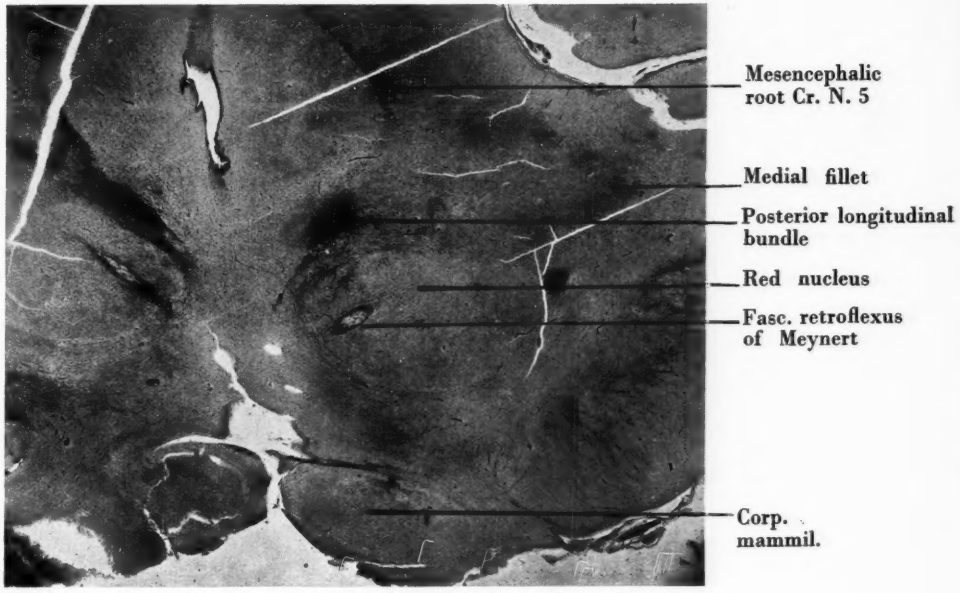

Fig. 10

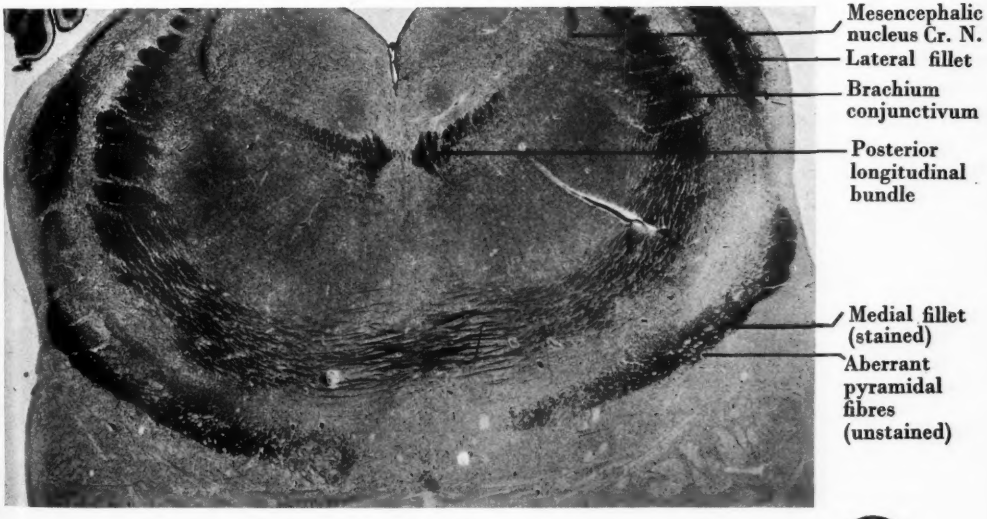

Fig. 11

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Fig. 12

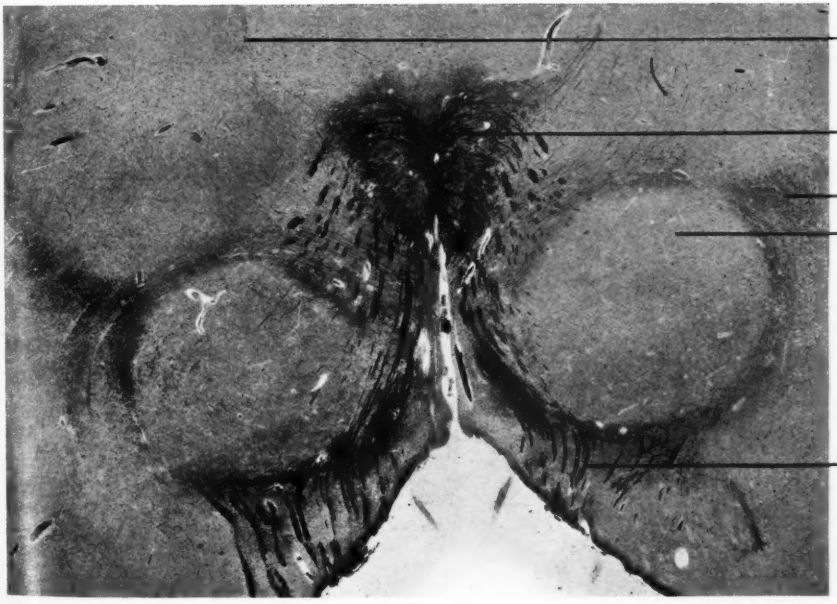

Fig. 13

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EXPLANATION OF PLATES

The figures are all untouched photographs of specimens stained by the Weigert-Pal method. The myelinated fibres appear black, as do also the capillaries.

Plate I

Fig. 1. T.S. Cervical region of cord. × 12. Foetus of 24–26 weeks. The myelination in the column of Burdach is very marked, and clearly heavier than that in the column of Goll. In addition, anterior and posterior root fibres are well myelinated. The myelination in the ground bundles shows particularly well owing to the absence of myelination in the adjacent tracts. Myelinated fibres crossing in the anterior commissure should be noted.

Fig. 2. T.S. Thoracic region of cord. × 9. Full-time foetus. The direct cerebellar tract, posterior columns and the ground bundles are intensely stained. The lack of myelination is very obvious in the direct and crossed pyramidal, rubro-spinal and olivo-spinal tracts.

Fig. 3. T.S. Thoracic region of cord. × 13. 36-week foetus. This section of low thoracic cord shows differences in staining in the two posterior columns, that of Burdach being more intensely stained than that of Goll. A very faint degree of myelination can be observed in Lissauer's tract; and the direct cerebellar tract is at this age well myelinated, though the staining exhibited is not so intense as in fig. 2 in full-time specimen. The absence of staining in the crossed pyramidal and rubro-spinal tracts is well seen.

Fig. 4. T.S. of medulla at mid-olivary level. × 9. Foetus of 28 weeks. (Lived 19 days and myelination further advanced than is usual in foetus of this age.) The myelination of sensory and connecting fibres is well shown, particularly in the solitary bundle, medial longitudinal bundle and fillet. The lateral part of the olive is devoid of myelinated fibres, whereas the medial and dorsal portions (older parts) have well myelinated connections.

Plate II

Fig. 5. T.S. Medulla. × 30. Full-time foetus. The section shows the origin of the 12th cranial nerve from its nucleus.

Fig. 6. T.S. Lower border of pons. × 9. Foetus of 26–28 weeks. The staining of the section is somewhat patchy, but the myelinated connection of the cochlear fibres of the 8th nerve with the superior olive can be well seen.

Plate III

Fig. 7. T.S. Lower border of pons. × 6. Full-time foetus. The 6th, 7th and 8th cranial nerves can be seen. When compared with fig. 6 it is clear that the myelination of the trapezium fibres is further advanced in this older specimen.

Fig. 8. T.S. showing nuclei of 5th cranial nerve. × 25. Full-time foetus. The large rounded cells of the mesencephalic nucleus are in sharp contrast with the multipolar cells of the motor nucleus. The lining epithelium of the fourth ventricle is shown at the left of the picture, and the mesencephalic root of the 5th nerve can be seen passing dorsally and lateral to the large cells.

Fig. 9. Section through subthalamic region. × 8. 28-week foetus. (Lived 19 days.) The myelinated fibres passing from the nucleus subthalamicus across the internal capsule to the striate body are well shown.

Plate IV

Fig. 10. T.S. mid-brain. × 8. 28-week foetus. (Lived 19 days.) The fasciculus retroflexus of Meynert is seen as a partially myelinated bundle of fibres in the red nucleus.

Fig. 11. T.S. At upper border of pons. × 11. Full-time foetus. In the posterior part of the section is seen the posterior longitudinal bundle medially, with the mesencephalic nucleus of the 5th nerve, the brachium conjunctivum and the lateral fillet laterally. The crossing of the brachia conjunctiva can be seen in the mid line, and still more anteriorly the medial fillet. Particularly noticeable are the unstained "aberrant pyramidal fibres" among the stained fillet fibres.

Plate V

Fig. 12. Section cut obliquely through the red nucleus. × 3½. Child of 8 months. The optic fibres are seen passing to the external geniculate body, and also sweeping round to the thalamus. The myelination of the pyramidal fibres in the crusta is still incomplete.

Fig. 13. Section through mid-brain. × 11. Full-time foetus. This section shows the fountain decussation of Meynert and the 3rd cranial nerve.

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Text-figure	Mag. given in Journal	Real mag.	Text-figure	Mag. given in Journal	Real mag.
1	25	31	9	25	31
2	100	122	10	100	125
2A	100	122	11	100	125
2B	100	122	12	100	125
3	25	31	13	100	125
4	25	31	14	100	130
5	100	125	15	100	82
6	25	31	16	100	82
7	100	125	20	100	81
8	100	125	24	100	84

The magnifications of text-figures 17, 18, 19, 21, 22, 23 and 25 are correct as printed.

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THE HISTORY OF THE PROCHORDAL PLATE IN THE RABBIT[1]

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INTRODUCTORY

This work has been carried out under the supervision of Prof. J. P. Hill to whom my sincere thanks are due, not only for his great help and criticism but also for allowing me access to the valuable series of rabbit embryos in his collection.

In all, ninety embryos, most of which are in a very good state of preservation, have been examined. The age, taken as the time lapsing between insemination and the removal of the embryo, ranges from eight to eleven days, but where possible the somites have been counted, and their number has been taken as indicating the degree of development. This method, however, does not seem to me to be the most exact. In fact the best criterion is a general survey of the degree of development of the structures present. The majority of the embryos were cut transversely, but a number were cut longitudinally. These have been of special value, and have enabled me to confirm the reconstructions made of transversely cut embryos.

DESCRIPTIVE

I propose to describe shortly the stages illustrating the history of the prochordal plate. The description will be made clearer by reference to the accompanying series of photomicrographs and reconstructions.

The earliest embryos examined are those of the head-process stage. In the two embryos representing this stage, the primitive knot, the primitive streak and the mesodermal sheet are already established. The prochordal plate presents the appearance shown in Plate I, fig. 1. It first makes its appearance 0·4 mm. behind the anterior border of the embryonal area and appears as a localised thickening of the endoderm. It does not seem to contribute to the mesoderm which reaches up to its lateral edges. The cells composing it are robust and compactly arranged, so that the plate is easily distinguishable from the endoderm on either side. Here and there a few flattened cells are seen on its under-surface.

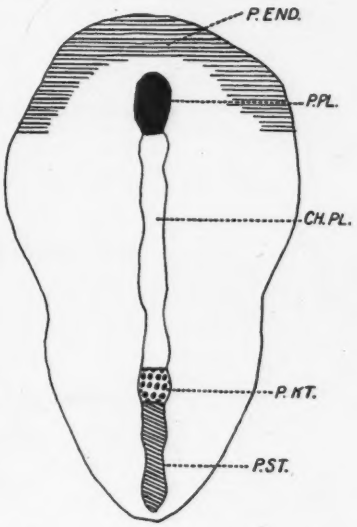
If this figure is compared with Plate I, fig. 2, which represents the 48th section behind fig. 1, the difference stands out clearly in so far as the relation

[1] Thesis approved for the degree of Master of Science in the University of London.

to the mesoderm is concerned. This is the head-process region and must not be confused with the prochordal plate. The presence of a mitotic figure on the right side and the apparent continuity with the mesoderm on the left seem to me to be very good evidence of the contribution of the head-process to the mesoderm. The appearance of this figure is also important, because later I shall produce figures, very similar to this, from an area between the definite prochordal plate and the definite chorda plate, which is marked (*I.Z.*) in the figures.

I should mention that in one of the embryos of the head-process stage the mesoderm is continuous across the middle line in front of the prochordal plate, while in the other, a rather poor specimen, it is not yet continuous, and we see the ectoderm overlying a thick patch of endoderm which extends across the whole breadth of the embryonal area in front of the prochordal plate.

This patch (*P.END.*) is however better marked in the next stage, which is shown in text-fig. 1. This is a dorsal view of an embryo with possibly one pair of somites and in which the axial structures are depicted. The crescentic shaded area in the figure (*P.END.*) represents a patch of thickened endoderm, the transverse part of which is co-extensive with the area between the prochordal plate (*P.PL.*) and the anterior border of the embryonal shield. It is prolonged backwards as two horns situated peripherally. The posterior limits are not easy to determine, but they extend some distance backwards. In this connection it is essential to state that Hubrecht has described in *Sorex vulgaris* the presence of an annular zone of thickened endoderm which is in continuity with the lateral margins of the prochordal plate and which he states proliferates to form vascular mesoderm. Assheton describes a similar area, which is, however, deficient posteriorly and which he calls the "pericardial thickening," in the rabbit.

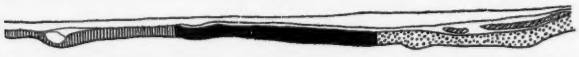


Text-fig. 1. A reconstructed dorsal view of embryo R 352, 8 days 1 hour, with possibly 1 somite. × 25.

The horseshoe-shaped zone of thickened endoderm (*P.END.*) here described, or rather its median part, lies cranially to the prochordal plate (*P.PL.*) as text-fig. 2 clearly shows. This figure also shows the presence of mesoderm (*P.M.*) between the ectoderm and the median part of the horseshoe-shaped endodermal thickening (*P.END.*), but whether the thickened endoderm contributes to this mesoderm or whether the latter is solely derived from the primitive

streak mesoderm, the horns of which grow forward and meet, cannot be decided in the stages examined. The further history of the antero-median part of the horseshoe-shaped endodermal thickening can be easily followed by the study of the reconstructed median longitudinal sections which are given here. It is important to note that with the forward growth of the brain accompanied by the development of the head-fold bay, the subsequent brain flexure and the backward growth of the pericephalic coelom, this antero-median area of thickened endoderm is seen to contribute to the floor of the fore-gut and to furnish the greater part of the endodermal element of the oral plate. Plate I, fig. 3, from an embryo with possibly one pair of somites, shows the prochordal plate to be in much the same condition as that shown in Plate I, fig. 1. It is also still the same, though shortened, in embryos possessing two somites and shown in text-figs. 2A and 2B. It is clear, however, that the mass of mesoderm (*P.M.*) is becoming thicker. I think it may rightly be called the "pre-axial mesoderm," since it is cranial to the prochordal plate (*P.PL.*), which is the most cranial axial structure.

Text-fig. 2. A reconstructed median longitudinal section of anterior end of same embryo as text-fig. 1. × 100.



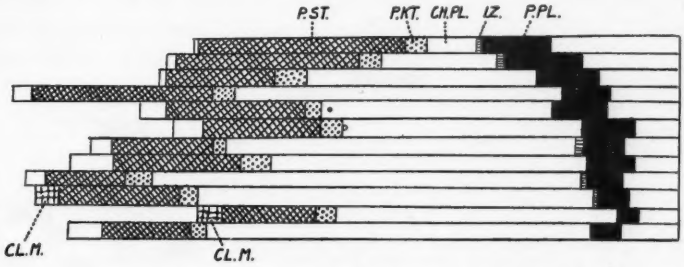
Text-fig. 2A. A reconstructed median longitudinal section of anterior end of R 339, 8 days, 2 somites. × 100.

Text-fig. 2B. A reconstructed median longitudinal section of anterior end of R 338, 8 days, 2 somites. × 100.

So far, the prochordal plate has been a one-layered structure, but in the stage possessing three pairs of somites it is several cells thick, cells having been proliferated on its upper side as is seen in Plate I, fig. 4. This figure also shows the two lateral horns of the thickened horseshoe-shaped endoderm situated towards the periphery of the embryonal area. They are made up of large cylindrical endodermal cells and are connected with the central prochordal plate by thin flattened endoderm. The mesoderm overlying the thickened endodermal horns is more compact than elsewhere, and in this as well as in the next embryos this compact mesoderm is found to follow the course of the horseshoe-shaped endodermal thickening. It is in this mesoderm that the pericardio-peritoneal coelom makes its appearance first in the region of the lateral

heart tubes in embryos with two pairs of somites. It extends forward and by the 5-somite stage it has become horseshoe-shaped with its transverse median part cranial to the prochordal plate. Van Beneden states that it is horseshoe-shaped from the beginning. It should be pointed out, however, that the earliest cavity to appear is the extra-embryonal coelom. It develops very early immediately behind the posterior end of the embryonal shield. The pericardio-peritoneal coelom is bilateral at first, and by the extension forward of its lateral halves and their union in front, the pericephalic coelom is established.

The horseshoe-shape of the thickened endodermal zone, the overlying compact mesoderm and the independence of both these structures from the prochordal plate are clearly shown in this embryo, but are illustrated from the next older stage—the 4-somite stage. I would like, however, to add that the horns of the horseshoe-shaped endodermal thickening become insignificant just before the region of the first pair of somites is reached.



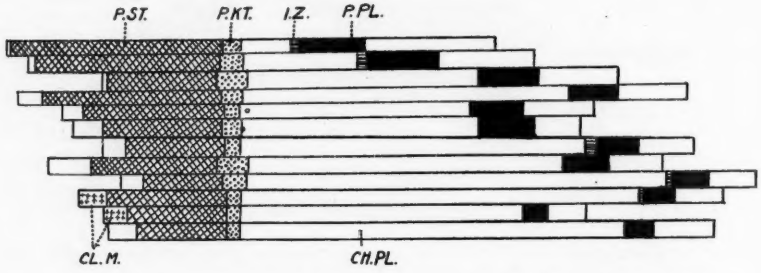
Text-fig. 3. Superimposed axes of twelve embryos with the anterior end as the fixed point. From above down they are: R 336, 8 days, no somites. R 353, 8 days 1 hour, no somites. R 352, 8 days 1 hour, ? 1 somite. R 349, 8 days 3 hours, 2 somites. R 338, 8 days, 2 somites. R 339, 8 days, 2 somites. R 314, 8 days 17¾ hours, 4 somites. R 357, 8 days 1 hour, 4–5 somites. R 343, 8 days 4 hours, 5 somites. R 318 A, 8 days 17¾ hours, 6 somites. R 316, 8 days 17¾ hours, 6 somites. R 346, 8 days 3 hours, 7 somites. × 25.

Before discussing the 4-somite stage I wish to refer briefly to text-figs. 3 and 4. These represent the structures in the median plane in each of the embryonal shields, which have been reconstructed in the same way as text-fig. 1. They are placed as shown in the figures with the anterior end as the fixed point in text-fig. 3 and the middle of the primitive knot as the fixed point in text-fig. 4. They range from the presomitic stage to the 7-somite stage. In all the prochordal plate is flat and the fore-gut has not yet closed.

Text-fig. 3 shows at a glance the remarkable fact that the prochordal plate (*P.PL.*) shortens with advance of age, while the chorda plate (*CH.PL.*) increases considerably in length. The significance of this will be discussed later, but it must be noted that this decrease in length of the prochordal plate is accompanied by an increase in thickness. In fact the first traces of this thickening are seen in Plate I, fig. 4. Any attempt, therefore, to explain the genuine shortening of the prochordal plate must not ignore the marked thickening it undergoes.

The second point to attract attention in text-figs. 3 and 4 is the apparent forward shifting of the prochordal plate (*P.PL.*) towards the anterior end of the embryonal area. This may be due to the unequal rate of growth of the parts concerned. Whether or not the shortening of the prochordal plate means contribution to the chorda plate is a question to be discussed.

The anterior end of the prochordal plate is practically always well defined from the antero-median part of the horseshoe-shaped thickened endoderm and the overlying compact mesoderm, but its junction with the chorda plate is not so readily determinable. In text-figs. 3 and 4, in a number of embryos, I have indicated a short axial segment intervening between the prochordal plate and the definite chorda plate (*I.Z.*). Its structure and relation to the mesoderm are shown in Plate II, fig. 8, and Plate III, fig. 14. Its cells are robust and closely packed, and at the sides are continuous with the mesodermal cells. The segment is usually one cell thick and contrasts markedly with the prochordal plate and the chorda plate. In appearance it very much resembles Plate I, fig. 2, which



Text-fig. 4. Same as text-fig. 3, but middle of primitive knot is taken as the fixed point. × 25.

passes through the head-process. I consider this segment, labelled *I.Z.*, as the last remains of the undifferentiated head-process, in fact its anterior end. If this view is correct, then the prochordal plate is not of head-process origin. This segment is shown in five embryos out of twelve, but its frequency is greater than that because in some cases, after having come to the conclusion that it is part of the head-process, I have included it with the chorda plate. It disappears later in older embryos, having become converted into chorda plate which becomes properly intercalated in the gut wall.

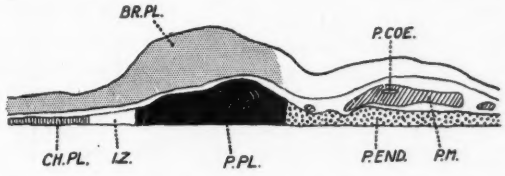
The shortening of the prochordal plate is relatively insignificant in comparison with the marked lengthening of the chorda plate. Even supposing the prochordal plate is diminished in length by reason of its transformation into chorda plate, a supposition which I believe is not true, the part added would be so small as to be insignificant.

Text-fig. 4 shows that the primitive knot (*P.KT.*) is more or less constant in extent, but the primitive streak (*P.ST.*) shortens as age advances.

It is perhaps worthy of mention here that the cloacal membrane (*CL.M.*) appears very late at the 6-somite stage immediately behind the primitive streak and not actually in its substance. The area behind the primitive streak in which it appears gradually increases in extent as age advances. The cloacal membrane (*CL.M.*) is shown in text-fig. 4 in the two embryos with 6 somites, but it is not yet distinguishable in the 7-somite embryo.

The two small circles situated just in front of the primitive knot in two of the embryos depicted in text-figs. 3 and 4 represent the ventral opening of the chorda canal, which is poorly developed in rabbit embryos.

Now we can come back to the 4-somite stage. A median longitudinal section of its anterior end is shown in text-fig. 5 and a dorsal view in text-fig. 6. In the latter the outlines of the horseshoe-shaped mesoderm, in the anterior part of which the pericephalic coelom (*P.COE.*) is not yet fully developed, are shown. The horns of this mesoderm, if followed back, will be found continuous with the primitive streak mesoderm (*P.ST.M.*). The pericardio-peritoneal coelom (*PP.C.*) is well developed in the region of the lateral heart tubes (*E.HT.*), but anteriorly, especially in the pre-axial mesoderm, it is in the form of isolated clefts. The

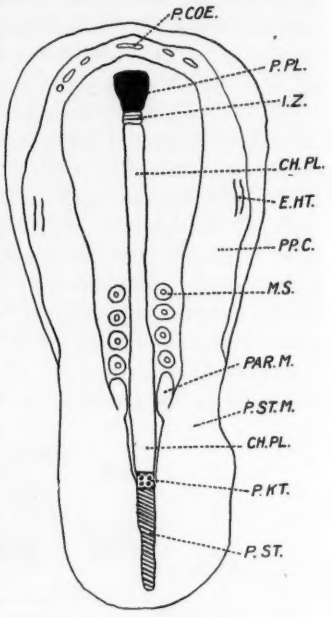


Text-fig. 5. A reconstructed median longitudinal section of R 314, 8 days 17¾ hours, 4 somites. × 100.

position of the lateral heart tubes (*E.HT.*) leaves no doubt of their independence from the prochordal plate (*P.PL.*) which latter is also independent from the pre-axial mesoderm (*P.M.*), as text-figs. 5 and 6 and Plate I, figs. 6 and 7, clearly show. When we examine text-figs. 2, 2 A, 2 B and 5 we find that the mass of pre-axial mesoderm (*P.M.*) is gradually increasing, and that in the last figure the pericardio-peritoneal coelom has appeared in the middle line, although its lateral extension is better appreciated by examining text-fig. 6.

The prochordal plate (*P.PL.*) has increased considerably in thickness and now appears in transverse section as a more or less triangular plate with cells piled on top of each other and well packed. The mesoderm on either side stops short of its lateral sides, and its cells contain chromatophilic granules in their cytoplasm. Its blunt apex produces an elevation in the middle of the neural plate, and curiously enough this elevation is replaced by a groove as soon as the caudal end of the prochordal plate is reached and we pass into that area between it and the definite chorda plate, regarded as the anterior end of the undifferentiated head-process (*I.Z.*). This area is well developed in this embryo, as can be gathered from text-figs. 5 and 6 and also from Plate II, fig. 8, which

also shows the last trace of the elevation caused by the prochordal plate. It also shows very clearly the continuity of the mesoderm with the remains of the head-process. Behind this area is the typical chorda plate. It is intercalated in the endoderm and does not show any continuity with the mesoderm on either side of it. To appreciate these points, Plate I, fig. 7, and Plate II, figs. 8 and 9, should be examined. The first figure is a typical section of the prochordal plate, the second passes through the remains of the head-process and the third through a typical chorda plate region.



Text-fig. 6. A reconstructed dorsal view of same embryo as text-fig. 5. × 25.

In front of the prochordal plate the relations of the parts are well shown in Plate I, figs. 5 and 6. In the former we see three layers spreading across the whole width of the embryonal area in that region. The endoderm is thick but is really made up of a layer one cell thick. The cells are large and cylindrical. This is the antero-median part of the horseshoe-shaped endodermal thickening. In Plate I, fig. 6, only 0·048 mm. behind fig. 5, the endoderm is beginning to resolve itself into the two horns connected here by a thinner patch of endoderm. The overlying mesoderm behaves like the endoderm in so far as it is resolved into two horns, as the two figures under consideration clearly show. In the mesoderm referred to the pericephalic coelom has appeared, but is not well developed. It has, where present, a thin dorsal and a thicker ventral wall.

A glance at the five figures—Plate I, figs. 5, 6, 7, and Plate II, figs. 8, 9—will convince one of the independence, already referred to, of the endoderm of the horseshoe-shaped thickening and the pre-axial mesoderm from the prochordal plate. This statement is further confirmed by Plate II, fig. 10, of a 5-somite embryo. It is as median a longitudinal section as possible and clearly shows the thickened endoderm at the anterior end of the embryonal area overlain by the compact pre-axial mesoderm, in which no definite pericephalic coelom has appeared. It is connected to the prochordal plate posteriorly by a thinner stretch of endoderm. The prochordal plate is only two cells thick and is not as well developed as in the 4-somite stage. This is, however, an individual variation.

The relations of the prochordal plate to the pre-axial mesoderm, the underlying thickened endoderm and the lateral heart tubes should be borne in mind. There is an interval between the anterior end of the prochordal plate and the

posterior border of the pre-axial mesoderm. This is seen in text-figs. 2, 2 A, 2 B and 5, and is confirmed by Plate I, fig. 6. Few cells occupy this interval and there is no indication that the prochordal plate contributes to the pre-axial mesoderm. It has, however, proliferated dorsally and has also shortened, a fact which may be explained by the contraction of the plate rather than by its transformation into chorda plate. Again, there is no evidence that the prochordal plate is contributing to the mesoderm on either side of it.

The endothelium of the lateral heart tubes may be derived either from the horns of the horseshoe-shaped endodermal thickening, or from the overlying compact mesoderm. The prochordal plate does not give any contribution to either the endothelium of the lateral heart tubes or the wall of the pleuro-pericardial coelom as was suggested by Hubrecht.

Embryos possessing five pairs of somites show little or no advance in the condition of the prochordal plate. Reference has already been made to Plate II, fig. 10. The pre-axial mesoderm is here clearly distinct both from the antero-median part of the horseshoe-shaped endodermal thickening and the prochordal plate. The prochordal plate here is two cells thick but is less massive than that of the 3-somite stage described above, though it is decidedly more advanced than that of the 2-somite stage.

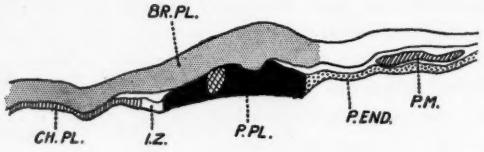
Plate II, fig. 11, is a longitudinal section, about 0·128 mm. from the median plane of another 5-somite embryo. It shows very well the compact mass of pre-axial mesoderm tending to be arranged in two layers, a thinner dorsal and a thicker ventral with a potential cavity between them. The contrast between this mesoderm and the more loose mesenchyme with which it is continuous posteriorly is very marked. The thickened endoderm, at the anterior end of the embryonal area and underlying the pre-axial mesoderm, is also very distinct. The prochordal plate (Plate II, fig. 12) is 2–3 cells thick, whereas this antero-median part of the horseshoe-shaped endodermal thickening is practically one cell thick, and while the latter is separated from the ectoderm by a compact darkly staining mass of pre-axial mesoderm, the former is not separated by any mass from the overlying ectoderm. There is in this specimen, as Plate II, fig. 12, shows, an apparent continuity between the anterior end of the prochordal plate and the pre-axial mesoderm, but as I have pointed out above this is not the usual arrangement, which is the more or less complete separation of the pre-axial mesoderm from the prochordal plate by an interval containing very few loose cells. I consider the condition seen here as simply an exaggeration of the usual arrangement. It must be remembered that the pre-axial mesoderm was already present in this region in the earliest embryos examined when the prochordal plate was one cell thick.

The next stage of a 5–6-somite embryo exhibits much the same condition as the preceding stages. Text-fig. 7 represents a reconstructed median longitudinal section of the anterior part of the embryo. It shows a well-developed prochordal plate (*P.PL.*) connected to the chorda plate (*CH.PL.*) by a segment, regarded as the remains of the undifferentiated head-process (*I.Z.*), but

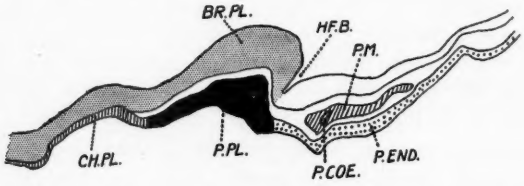
anteriorly it is separate from the pre-axial mesoderm (*P.M.*) in which the pericephalic coelom is not yet continuous across the middle line. The ectoderm is decidedly thicker and is elevated over the prochordal plate area in the middle line. The latter shows an isolated mass of cells in its caudal half of unknown significance.

Beneath the anterior end of the prochordal plate there are three cells which are considered as degenerating cells of prochordal plate origin. Few mitotic figures are present in it, and again there is no evidence that it contributes to the mesoderm on either side of it.

It is a noteworthy fact that, whilst the prochordal plate undergoes definite changes, particularly in thickness, the antero-median part of the horseshoe-shaped endodermal thickening (*P.END.*) does not show any change in form, thickness or extent.



Text-fig. 7. Anterior part of a reconstructed median longitudinal section of R 343, 8 days 17¾ hours, 5 somites. × 100.

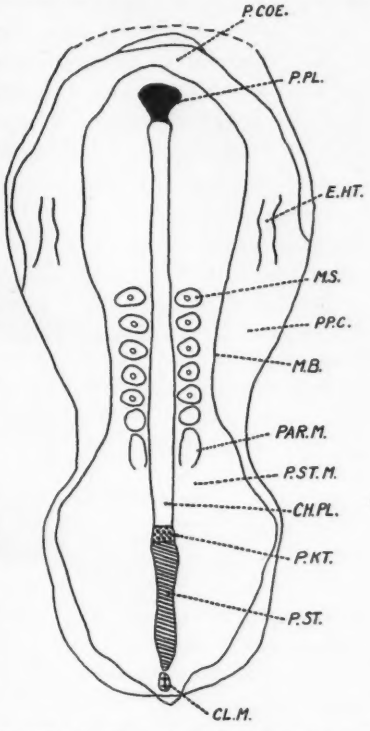


Text-fig. 8. Anterior part of a reconstructed median longitudinal section of R 346, 8 days 3 hours, 7 somites. × 100.

Now we pass on to a slightly older stage which is represented by text-fig. 8, the anterior end of a reconstructed median longitudinal section of a 6–7-somite embryo. The anterior part of the prochordal plate is more massive than its posterior part. Its caudal extremity corresponds with the point where the elevation in the ectoderm, referred to above, gives place to a groove. The head-fold bay (*HF.B.*) is beginning to appear just cranial to this elevation in the middle of the neural plate over the extent of the prochordal plate. This latter shows chromatophilic granules, but there is no proliferation of mesoderm from its lateral margins. Mitotic figures are not specially abundant, and in this embryo some degenerated cells are scattered here and there beneath the main mass of the plate. There is a short segment, the remains of the head-process, which extends through 2–3 sections and which, in the figure, has been included with

the chorda plate (*CH.PL.*). The distinctive features of the prochordal plate, apart from its thickness and position, are the presence of the chromatophilic granules and the compact arrangement of its cells.

Text-fig. 9 is a reconstruction of the dorsal view of a 6-somite embryo, and text-fig. 10 is a median longitudinal reconstruction of the anterior part of the same embryo. The pericephalic coelom (*P.COE.*) is well developed and the preaxial mesoderm (*P.M.*) in which it is developed is in close contact with the endoderm just in front of the anterior end of the prochordal plate (*P.PL.*). The latter is very well developed and it is now many cells in thickness. It is triangular in both the coronal and sagittal planes, as is clearly seen in text-fig. 10 and Plate II, fig. 13. The elevation presumably produced by this plate in the middle of the neural plate is also well shown in both figures. The plate shows the characteristic chromatophilic granules (Plate II, fig. 13) and does not contribute to the mesoderm on either side. On the right of this figure one can see a thin endoderm layer connecting the prochordal plate with the right horn of the horseshoe-shaped endodermal thickening underlying the pericardio-peritoneal coelom. The latter has a thin roof and a thick floor between which and the endoderm is a thin strand of angioblastic cells. The endothelial heart tubes (*E.HT.*) are well developed, as can be seen in text-fig. 9. The head-fold bay (*HF.B.*) is well established, as seen in text-fig. 10.



Text-fig. 9. Reconstructed dorsal view of R 318A, 8 days 17¾ hours, 6 somites. × 25.

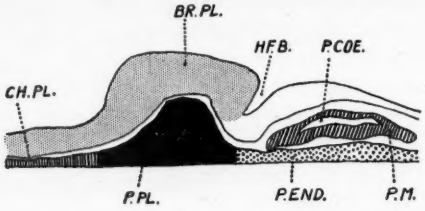
Plate III, fig. 14, passes through the cranial segment of the head-process and shows very well its relations to the mesenchyme, especially on the right side. In this figure the dorsal furrow has replaced the median elevation which was seen in the region of the prochordal plate in Plate II, fig. 13. Plate II, fig. 13, and Plate III, figs. 14 and 15, show the prochordal plate, the remains of the cranial segment of the head-process and the chorda plate respectively, and should be compared with Plate I, fig. 7, and Plate II, figs. 8 and 9.

In the dorsal view—text-fig. 9—the outlines of the pericardio-peritoneal coelom (*PP.C.*) and its pericephalic part (*P.COE.*) are well shown. It communi-

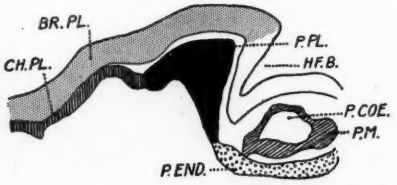
cates in the region of the first somite with the extra-embryonal coelom, and immediately behind the last somite its inner limit (*M.B.*) lies very near the margin of the embryonal area.

It may be noted that the cloacal membrane (*CL.M.*) makes its first appearance in this stage immediately behind the posterior end of the primitive streak and not in its substance as some observers claim.

Some progress has manifested itself in the next stage, although it possesses the same number of somites as the preceding. Text-fig. 11 shows a well-developed head-fold bay (*HF.B.*) and an apparent caudal displacement of the pre-axial mesoderm (*P.M.*), its contained pericephalic coelom (*P.COE.*) and



Text-fig. 10. Anterior part of a reconstructed median longitudinal section of R 318 A. × 100.



Text-fig. 11. Anterior part of a reconstructed median longitudinal section of R 316, 8 days 17¾ hours, 6 somites. × 100.

the underlying thickened endoderm of the horseshoe-shaped area (*P.END.*). The prochordal plate (*P.PL.*) is well marked and has a triangular shape in the sagittal plane. It occupies the angle between the neural plate and the upper layer of the head-fold bay and forms the roof of the incipient fore-gut bay. This stage is important because it shows us the beginning of the establishment of the anterior position of the prochordal plate, which is better seen in text-fig. 12.

In preceding stages the pre-axial mesoderm was situated in practically the same plane as the prochordal plate, but with the establishment of the head-fold bay and the forward growth of the neural plate, the pre-axial mesoderm and the underlying endoderm of the horseshoe-shaped area now occupy a more ventral plane than the prochordal plate, although they are still anterior to it. The tip of the angle between the neural plate and the upper layer of the head-fold bay lies opposite the posterior third of the pre-axial mesoderm, whereas

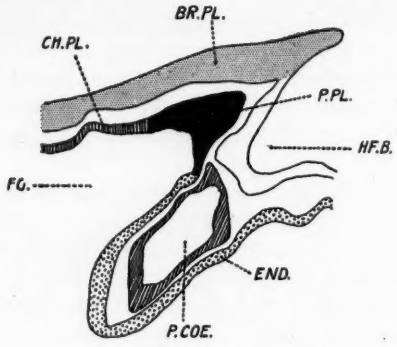
in the previous embryo it lies just behind its posterior end. These alterations in the relations of the prochordal plate are the outcome of the commencing formation of the fore-gut, and that, as K. M. Parker has pointed out in her paper on the early development of the heart in marsupials, would appear to be induced by the forward growth of the brain plate, the backward extension of the pre-axial mesoderm and its contained coelom, and the gradual incorporation into the latter of the bilateral pericardial cavities.

Plate III, fig. 16, showing a median longitudinal section of a 7-somite embryo, affords confirmation of the general correctness of the last four text-figures, which are reconstructions made from transverse series. It much resembles text-fig. 11, the projection formed by the main mass of the prochordal plate being a striking feature. The posterior limit of the prochordal plate is not so easy to make out here as in the transverse sections, in which the characteristic appearance of the cranial segment of the head-process serves as a good landmark. Its anterior end passes into the antero-median part of the horseshoe-shaped endodermal thickening, overlying which is the pre-axial mesoderm with its pericephalic coelom. I have mentioned above, however, that there is a thinner patch of endoderm between the prochordal plate and the antero-median thickened endoderm referred to. This is the usual arrangement. The elevation of the anterior part of the brain plate as well as the head-fold bay are well marked.

Between the floor of the pericephalic coelom and the underlying thickened endoderm there are found two angioblastic cells, the origin of which is not easy to decide, but they appear to be mesodermal. There is no evidence of proliferation on part of the endoderm.

The changes that have been described above have made further progress in the next stage possessing 8–9 pairs of somites. A reconstructed median longitudinal section is shown in text-fig. 12. Here the head-fold bay (*HF.B.*) is more marked than before, the brain plate (*BR.PL.*) has grown forward considerably and the pericephalic coelom (*P.COE.*) now lies further back, its anterior or cranial wall lying a little caudal to the free tip of the prochordal plate (*P.PL.*) which still occupies the angle between the brain plate (*BR.PL.*) and the upper layer of the head-fold bay. The fore-gut (*FG.*) is established, its length being 0·112 mm. Examination of text-figs. 8, 10, 11 and 12 will convince one that its floor is formed by the antero-median part of the horseshoe-shaped endodermal thickening. The prochordal plate (*P.PL.*), however, forms the anterior wall of the fore-gut and a very small part of the adjoining roof. Perhaps this will be better understood if we were to unfold the bends caused by the head-fold bay and the closed gut. If we do that we should obtain a figure very much like text-fig. 10. In this way we can realise how the endoderm of the thickened zone, originally anteriorly situated, has come to form the floor of the fore-gut, with the result that the prochordal plate comes to be the most anterior or cranial endodermal structure. As the reconstruction shows there are no foldings or evaginations in the fore-gut wall where it is formed by the prochordal plate.

Text-fig. 12 shows the relations of the massive prochordal plate. The plate lies mainly in the angle between the brain plate and the upper layer of the head-fold bay. Its tip is free and it gradually increases in depth as it is traced caudally. It forms the anterior wall of the fore-gut and the adjoining part of the roof, but does not enter into the formation of the floor of the fore-gut. Caudally it passes into the chorda plate (*CH.PL.*) without the intervention of a head-process segment. There is a distinct space between the dorsal surface of the prochordal plate and the neural plate (*BR.PL.*). The latter does not exhibit any elevation in the middle line such as was observed in earlier stages. The prochordal plate is solid and massive, measuring about 0·112 mm. in length, 0·088 mm. in greatest depth and 0·088 mm. in greatest width. Its cells are compactly arranged (Plate III, figs. 18 and 19) and show a tendency, especially on the left side, to proliferate mesoderm. In Plate III, fig. 19, there is an apparent vesicular structure to the left of the prochordal plate and in apparent



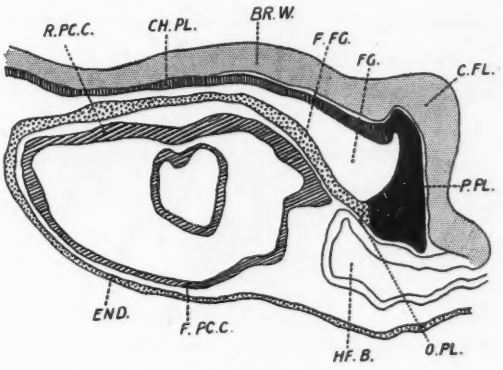
Text-fig. 12. Median reconstruction of R 324, 8 days 17¾ hours, 8–9 somites. × 100.

continuity with it, but composed of less compactly arranged cells. On the right of the plate, in a nearly corresponding position, there is a more or less rounded mass of cells which appears in three successive sections. I have not found comparable masses in any of the other embryos examined. The facts, just pointed out, are clearly observed in Plate III, figs. 17, 18, 19 and 20, which are four successive sections of the same embryo. The brain is still flat and the chorda plate is still intercalated in the gut endoderm.

A further change has manifested itself in the next stage. The primary brain flexure is now quite prominent, as can be seen in text-fig. 13 and Plate III, fig. 21. The neural tube is closed from just behind the cephalic flexure to the region of the first somite. Text-fig. 13 is from a median longitudinal section of a 9–10-somite embryo. It shows how the flexure in the brain has influenced the form of the prochordal plate (*P.PL.*). It lies in close contact with the brain wall and with the upper layer of the head-fold bay. It is, therefore, still situated in the angle between the anterior part of the wall of the brain and the upper

layer of the head-fold bay, as in text-fig. 12, in which the flexure was much less obvious. The prochordal plate forms the anterior wall of the fore-gut (*FG.*), but only a very small part of the dorsal wall. Just at the angle where the very short dorsal moiety of the plate passes into the extreme anterior part, there is a slight evagination which I believe to be the homologue of Seessel's pouch. Its walls are accordingly formed by the prochordal plate. Besides this, there are no other foldings or evaginations in the region of the plate. Streeter observed several foldings in the pig and homologised the folded prochordal plate with the "Gaumentasche" of Selenka.

The oral plate (*O.PL.*) is now established, its ectodermal and endodermal elements being in contact but individually distinguishable. It lies immediately caudal to the prochordal plate and just cranial to the pericardial cavity. Its



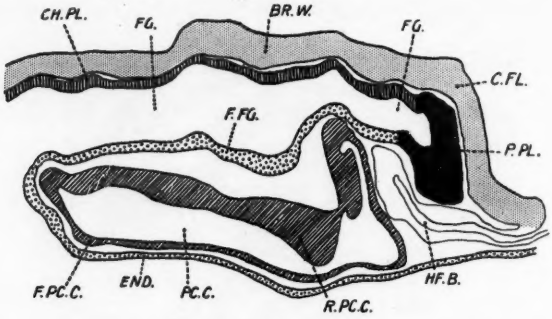
Text-fig. 13. Median reconstruction of R 321, 8 days 17¾ hours, 9–10 somites. × 100.

ectodermal element is formed by the caudal part of the upper layer of the head-fold bay. The endodermal element of the oral plate is directly continuous with that of the prochordal plate. The posterior two-thirds of the oral plate endoderm are to my mind derived from the antero-median part of the horseshoe-shaped endodermal thickening. The cranial third, however, may receive contributions from the prochordal plate. These statements can be verified by examining the figures.

Text-fig. 13 shows that the ventral part of the prochordal plate (*P.PL.*) is more massive than its dorsal part. There is as yet no trace of the buccal hypophysis, and the pericardial cavity has been pushed further back and is quite huge. The chorda plate (*CH.PL.*) is still intercalated in the roof of the gut, and in many places is in very close contact with the floor of the neural tube.

The reconstruction shown in text-fig. 13 should be compared with Plate III, fig. 21, which is a photomicrograph of the anterior end of a median longitudinal section of an embryo possessing 9 somites. It is practically identical

with text-fig. 13. Note the very close contact between the brain wall and the thick prochordal plate. The latter is also in contact with the upper layer of the head-fold bay and forms the anterior wall of the fore-gut. It also forms the dorsal angle of the fore-gut where there is an evagination—Seessel's pouch—the wall of which is of prochordal plate derivation. The ventral angle of the fore-gut shows the continuity of the prochordal plate with the thick endoderm of the oral plate. The latter is pale compared with the darker staining prochordal plate in which are chromatophilic granules, absent in the oral plate endoderm. Immediately behind Seessel's pouch the prochordal plate runs into the chorda plate which is one cell thick and in contact with the floor of the neural tube. Caudal to the oral plate and the fundus of the head-fold bay the pericardial cavity is seen with thick roof and thin floor.



Text-fig. 14. Median reconstruction of R 320, 8 days 17¾ hours, 10–11 somites. × 100.

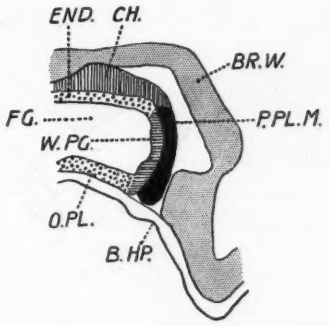
Practically the same relations are shown in the next older stage which possesses 10–11 pairs of somites. Text-fig. 14 resembles text-fig. 13 in the salient points. The prochordal plate lies immediately behind the flexed brain wall and forms the anterior wall of the fore-gut which is considerably thicker than the other walls. It extends slightly laterally and shows chromatophilic granules in the cytoplasm of its cells. Its intimate relation with the flexed wall of the fore-brain should be borne in mind, since in the next stage to be described this comes to an end and a space filled with mesenchyme is present between the two. The oral plate is not well seen, probably owing to the sectional plane.

The notochord is not yet separated, at least in the area shown here. The fore-gut is extensive and the roof of the pericardial cavity (*R.PC.C.*) is now very thick, whereas the floor is very thin (*F.PC.C.*).

The anterior end of the chorda plate (*CH.PL.*) passes into the prochordal plate (*P.PL.*), but it is practically impossible to locate the limits of the latter accurately because there is always some difficulty about one or two sections at the ends of the plate where it passes into the oral plate endoderm and the chorda plate respectively.

We may pass on to a stage with 14–15 somites, since there are no noteworthy changes in the interval. Important advances have now been made as text-fig. 15 shows. The chorda (*CH.*) has separated from the endoderm but is still in close contact with both brain wall (*BR.W.*) and gut roof (*END.*), except at its most anterior end which terminates in the prochordal plate just cranial to the meeting of the roof of the gut and its anterior wall (*W.PG.*). I should state that it has started to separate in the 13-somite stage.

The prochordal plate shows partial delamination into its two important derivatives which are the anterior wall of the gut (*W.PG.*) and the prochordal mesoderm (*P.PL.M.*). These are still in close contact as the reconstruction shows, but can be identified as separate structures, except perhaps dorsally, where the chorda passes into the prochordal plate. The ventral portion of the prochordal plate mesoderm appears as a thickened mass which is practically separate from the wall of the gut as Plate III, fig. 22, shows. It is situated—

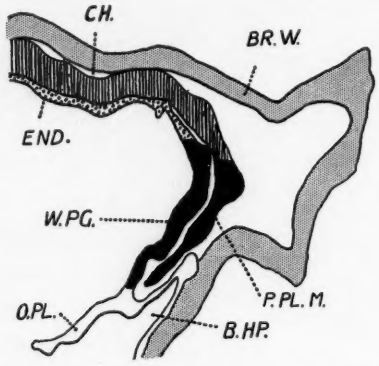


Text-fig. 15. Median reconstruction of R 179, 8 days 19 hours, 14–15 somites. × 100.

text-fig. 15—between the oral plate (*O.PL.*) caudally and the brain wall cranially, and cranio-ventral to it lies the primordium of the buccal hypophysis (*B.HP.*). As Plate III, fig. 22, shows, it differs in appearance from the mesenchyme on either side of it, the cells stain more deeply, are more closely packed and frequently contain chromatophilic granules. This mass appears to be the homologue of that part of the prochordal mesoderm from which in other forms the premandibular somites arise. It may be referred to as the premandibular somitic mass or, shortly, as the premandibular primordium. Its position in front of the oral plate, here well developed, as well as its relation to the hypophysis, which will be better seen later, entitles it to be so homologised. It is more massive than the thinner strand of prochordal mesoderm which connects it with the anterior end of the chorda (*CH.*). There are no cavities either in the mass itself or in its lateral extensions when these are present, and in putting forward this view of its homology, I lay stress on its position, origin and relations. Its fate will be described later.

The appearance of a space occupied by mesenchyme between the prochordal plate and the brain wall is another striking feature of this stage. In the preceding stage the prochordal plate and the brain wall were in close contact. It may be that the appearance of this space is due to the fact that the brain is growing more rapidly than the adjoining structures, particularly the prochordal plate. The origin of the mesenchyme which fills the space is of interest. It is either proliferated from the prochordal plate or is formed by the medial growth of the laterally situated mesenchyme. The latter is the most probable origin, but it is probable that the prochordal plate contributes to it in part.

The oral plate (*O.PL.*) is well established and its two layers are still quite distinct. The primordium of the buccal hypophysis (*B.HP.*) is just indicated cranial to the oral plate and ventral to the mass of presumed premandibular mesoderm. The anterior part of the chorda (*CH.*) is somewhat thickened, but there are no lateral proliferations in connection with it.



Text-fig. 16. Median reconstruction of R 253, 9 days 10 hours, 21 somites. × 100.

It is accordingly in the stages between 14 and 16 somites that the changes above described manifest themselves. They are uniformly exhibited in the ten embryos of this stage which I have examined.

Further progress in the same direction has taken place in the next stage, represented by an embryo aged 9 days 10 hours and possessing 21 pairs of somites. If, however, text-fig. 16, representing this stage, is compared with the preceding text-figure, it will be noticed that nothing of great importance has happened in the interval.

The buccal hypophysis (*B.HP.*) is well established, is in close contact with the brain wall, and is widely open. The oral plate (*O.PL.*) is very thin but is still intact. The chorda, separate as before, ends anteriorly in the strand of prochordal mesoderm (*P.PL.M.*) which is practically completely separate from the anterior wall of the fore-gut (*W.PG.*), in fact a narrow space exists between them. The process which began in the 14–16-somite stage is here more or less

complete and has resulted in the transformation of the prochordal plate into a strand of prochordal mesoderm (*P.PL.M.*) and the anterior wall of the fore-gut (*W.PG.*). The mesenchyme-filled space in front of the prochordal mesoderm is considerably increased in extent as compared with text-fig. 15.

The structure and relations of the prochordal mesoderm are shown in Plate IV, figs. 23 and 24. In the former we see a median cellular strand situated between the brain walls. The very short and thin upper part of this is formed by the chorda, whilst the remainder, much thicker and more or less irregular, is formed by prochordal mesoderm in which the chorda ends. It contains granules which are, however, not well shown in this section. If we compare this figure with Plate III, fig. 18, we at once see the difference in size of the prochordal plate. This, together with the irregular appearance of the prochordal mesoderm, suggests that it contributes to the mesenchyme. Indeed, in the later stages we shall find that the whole prochordal mesoderm is converted into mesenchyme. The solid compact mass which lies to the right of the prochordal mesoderm is the cut wall of the fore-gut and has nothing to do with the prochordal plate.

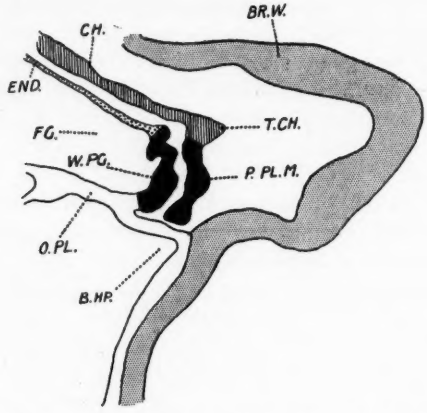
Plate IV, fig. 24, is 0·112 mm. behind Plate IV, fig. 23. The separated chorda is clearly seen between the roof of the gut and the floor of the brain, whilst between the floor of the gut and the posterior wall of the buccal hypophysis is a horizontally disposed, flattened, plate-like strand of cells, readily distinguishable by its darkly staining character. If this strand is examined it will be seen that it really consists of a small median mass and two lateral extensions, slightly asymmetrical, the left one being the larger of the two and possessing a small lumen round which the cells are radially arranged. When the median part is followed in the series it is found to become continuous with the prochordal strand of mesoderm seen in Plate IV, fig. 23—see the reconstruction, text-fig. 16. This median mass is accordingly to be regarded as none other than the premandibular somitic mass seen in the preceding stage, whilst its lateral extensions, if that interpretation is correct, are to be regarded as rudimentary premandibular somites.

The net result, therefore, is the transformation of the prochordal plate into prochordal mesoderm and the anterior wall of the pre-oral part of the fore-gut. Dorsally the chorda ends in the slender median prochordal mesoderm, which is expanded ventrally to form the premandibular mass from which rudimentary premandibular somites may arise. This process takes place by delamination as can easily be made out by examining text-figs. 14, 15 and 16.

The delamination is almost complete in the next stage, shown in text-fig. 17, which is a reconstruction made from the longitudinal sections, while Plate IV, fig. 25, shows a nearly median longitudinal section of the same embryo aged 9 days 16 hours and possessing 23–24 pairs of somites. The oral plate (*O.PL.*) is deficient in places, and it is now difficult to identify ectoderm and endoderm as separate layers. The prochordal mesoderm (*P.PL.M.*) is clearly seen in front of the anterior wall of the fore-gut (*W.PG.*) which is made up of columnar epithelium and is therefore thicker than the dorsal wall made of cubical

epithelium (*END.*). Chromatophilic granules are seen in the cytoplasm of the cells of the prochordal mesoderm, particularly in its ventral part, which extends out laterally on either side of the median plane, as can be ascertained by examining the sections. The dorsal part of the prochordal mesoderm, however, appears in 2–3 sections only and in it the notochord (*CH.*) ends cranially to the wall of the gut. The chorda (*CH.*), quite separate from the brain wall and the roof of the fore-gut, shows a free anterior tip (*T.CH.*) which is better marked in later stages. There are no chromatophilic granules in the chorda at all.

It is not out of place here to state that the intercalated chorda plate separates from the gut wall either by evagination of the plate and the approximation of the edges of the endoderm, or simply by the approximation of these edges beneath the chorda plate. These two different methods may take place in one and the same embryo.



Text-fig. 17. Composite outline drawing of anterior part of R 248, 9 days 16 hours, 23–24 somites. × 100.

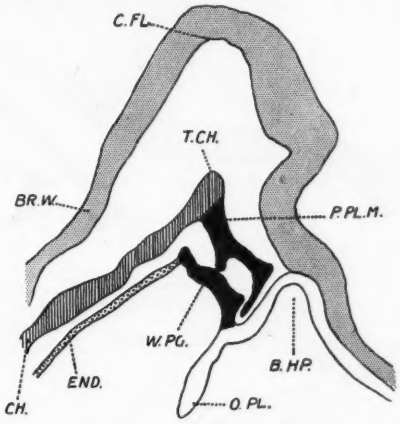
No cavities occur in the prochordal mesoderm, nor is there any definite proliferation from the slender strand which connects the swollen ventral part with the chorda. The whole prochordal mesoderm (*P.PL.M.*) corresponds to what Oppel calls "Praechordalplatte," and its swollen ventral part has been here called the premandibular primordium. The space which lies cranially to the prochordal mesoderm and which is filled with loose mesenchyme is greater than before.

I referred above to the fact that the anterior end of the chorda extends forward as a free tip beyond the connection with the prochordal mesoderm (*P.PL.M.*). This is better seen in text-fig. 18, which is a composite outline drawing of the anterior end of an embryo aged 9 days 10 hours and possessing 24 somites. The median sections are shown in Plate IV, figs. 26 and 27.

The prochordal mesoderm (*P.PL.M.*) occupies its usual position but is more

irregular and much looser than in the preceding stage (compare Plate IV, figs. 25, 26 and 27). It is connected by a bridge to the anterior wall of the pre-oral part of the fore-gut (*W.PG.*), but apart from that it is quite free from both the gut wall (*W.PG.*) and the buccal hypophysis (*B.HP.*). Here again its ventral part extends laterally on either side of the median plane, whereas the strand connecting it with the chorda is quite thin, extending through only 2–3 sections in the median plane itself. Chromatophilic granules are present in the prochordal mesoderm (*P.PL.M.*) as well as in the anterior wall of the fore-gut (*W.PG.*), but only two mitotic figures were observed in the whole extent of the mass.

If we examine text-fig. 18 and Plate IV, figs. 26 and 27, we see at once that the freely projecting cranial tip (*T.CH.*) of the chorda is now more marked. It is in active growth as shown by the presence in it of mitotic figures. This is evidence of the independence of the chorda from the prochordal mesoderm. The



Text-fig. 18. Same as text-fig. 17 from R 255, 9 days 10 hours, 24 somites. × 100.

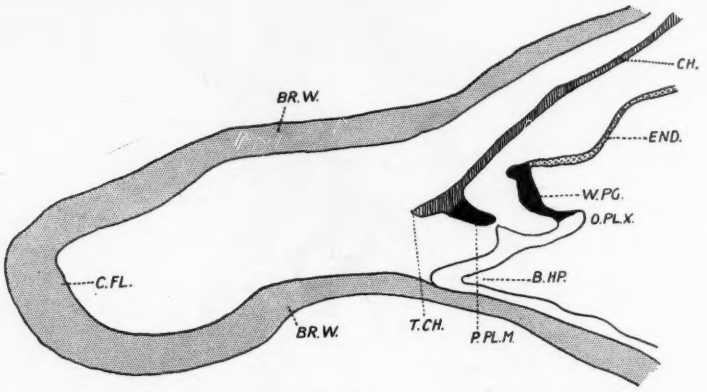
latter reaches down to the apex of the angle between the anterior wall of the fore-gut (*W.PG.*) and the posterior wall of the buccal hypophysis (*B.HP.*).

In text-fig. 18 a projection of the anterior wall of the fore-gut (*W.PG.*) is seen to be directed towards the posterior wall of the buccal hypophysis (*B.HP.*) from which a similar projection arises but does not appear in the figure since the projections are separated by prochordal mesoderm. More laterally they meet but do not fuse together. Certain authors, Kupffer, Atwell, Miller and Parker, state that the endoderm of the fore-gut contributes to the hypophyseal primordium, but, beyond the relationship just described, I have seen no evidence of any contribution from the anterior wall of the fore-gut (*W.PG.*) to the hypophysis in the rabbit.

The next stage, an embryo possessing 27 pairs of somites and aged 10 days 18 hours, is represented by text-fig. 19, which is a composite outline drawing. The brain has increased greatly in size, so that the bay resulting from the cranial

flexure is much enlarged and the oral plate has entirely disappeared. The cranial extremity of the chorda now presents a bifid appearance, but only the dorsal limb (*T.CH.*) belongs to the chorda and represents its freely projecting tip. The ventral limb is really formed by a pointed mass of prochordal mesoderm (*P.PL.M.*), all that is now left of it. The remainder of this structure, including its swollen ventral part, has been practically completely converted into mesenchyme. All the evidence is against the ventral part of the apparent bifid chorda being regarded as a chordal extension. Grünwald, Tourneux, and Keibel gave figures of apparent bifid chorda, but the explanation given above seems to me the only one possible.

In text-fig. 19 it will be seen that the tip of the prochordal mesoderm remnant (*P.PL.M.*) nearly comes in contact with a projection from the posterior wall of the buccal hypophysis. There is an attempt at a third projection



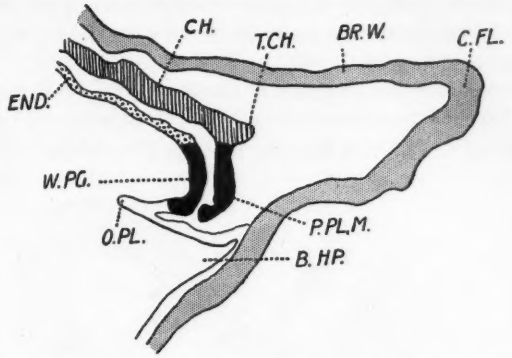
Text-fig. 19. Same as text-fig. 17 from R 281, 10 days 18 hours, 27 somites. × 100.

from the anterior wall of the pre-oral gut (*W.PG.*) which is here very well developed. It is still thicker than the rest of the fore-gut wall (*END.*).

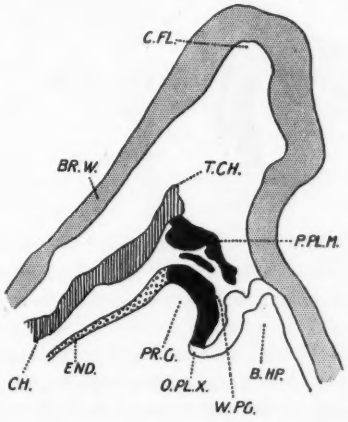
The next stage is shown in text-fig. 20 and is that of an embryo possessing 27–28 somites and aged 9 days 16 hours. The prochordal mesoderm (*P.PL.M.*) is a thin strand of cells containing chromatophilic granules and extending between the chorda dorsally and the posterior wall of the buccal hypophysis ventrally. It is irregular in its outline and I believe it is contributing to the mesenchyme. Its ventral part is definitely mesenchymatous on one side of the median plane, while on the other it consists of more closely packed cells containing granules. We have here the last remnant of the premandibular mass. Note the free tip of the chorda (*T.CH.*) which shows mitotic figures.

The oral plate has practically completely disappeared, leaving only a remnant (*O.PL.*) at the angle where the endoderm of the pre-oral part of the fore-gut passes into the ectoderm.

Text-fig. 21 does not show much advance over the previous stage. It is a composite outline drawing of an embryo possessing 28–29 somites and aged 10 days 1 hour. Again the free tip of the chorda (*T.CH.*) shows mitotic figures indicative of growth at this point. The strand of prochordal mesoderm is not compact, is irregular in outline and seems to be changing into



Text-fig. 20. Anterior part of a reconstructed median longitudinal section of R 246, 9 days 16 hours, 27–28 somites. × 100.

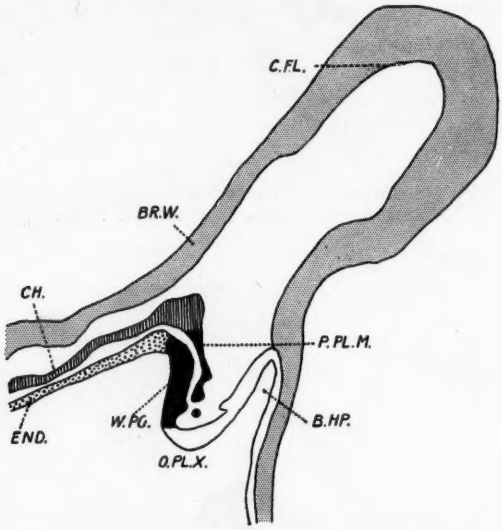


Text-fig. 21. Composite outline drawing of anterior part of R 277, 10 days 1 hour, 28–29 somites. × 100.

mesenchyme. Between its main mass (*P.PL.M.*) and the anterior wall of the pre-oral part of the fore-gut (*W.PG.*) there is a detached mass of prochordal mesoderm. It contains chromatophilic granules and much resembles the same mass in Plate IV, fig. 26, but its ventral part is not swollen; the whole mass extends through 2–3 sections.

So far the chorda has not come in direct relation with the hypophysis. They are linked together by the prochordal mesoderm (***P.PL.M.***).

What is practically the last stage in the history of the prochordal mesoderm is shown in text-fig. 22 and Plate IV, figs. 28 and 29. The embryo from which these are taken possesses 30 pairs of somites and is $10\frac{1}{2}$ days old. Text-fig. 22, which is a composite outline drawing, shows that the oral plate has completely disappeared and that the mesenchyme-filled space cranial to the pre-oral part of the fore-gut has increased in extent. Immediately in front of the gut wall (***W.PG.***) we come across the remnant of the prochordal mesoderm (***P.PL.M.***) in the form of a thin strand stretching from the anterior end of the chorda (which is devoid of a projecting free tip), down to the angle (***O.PL.X.***) bounded



Text-fig. 22. R 282, $10\frac{1}{2}$ days, 30 somites. × 100.

by the posterior wall of the buccal hypophysis and the anterior wall of the fore-gut (***W.PG.***). It extends through only two sections as a thin compact strand of cells. Its ventral part, which was homologised with the premandibular primordium, has been largely converted into mesenchyme. Close on either side of the middle line in the region of the ventral swollen mass of earlier stages one encounters a blood vessel surrounded by mesenchyme.

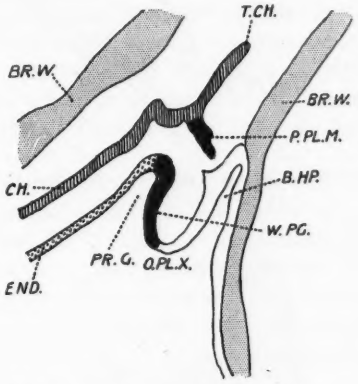
The tip of the chorda lies cranially to the angle between the anterior (***W.PG.***) and the dorsal (***END.***) walls of the fore-gut. No mitotic figures are visible in it.

Text-fig. 23 is a median reconstruction made from the longitudinal sections of the anterior end of an embryo of 11 days and possessing 37 somites. The chorda has now grown forward to a much greater extent than in any of the

preceding embryos, as is indicated by the position of the remnant of the prochordal mesoderm (*P.PL.M.*) which is in continuity with its ventral side some distance behind its tip (*T.CH.*). The prochordal mesoderm takes the form of a small more or less irregular strand composed of loosely arranged cells which extends through two sections, one of which is shown in Plate IV, fig. 30.

Here again a projection of the posterior wall of the buccal hypophysis (*B.HP.*) is seen directed towards the prochordal mesoderm remnant (*P.PL.M.*). It is very similar to that shown in text-fig. 19. In fact the two stages closely resemble each other save for the greater forward extension of the chorda in text-fig. 23.

The buccal hypophysis is still widely open (*B.HP.*), and the oral plate has completely disappeared. The anterior wall (*W.PG.*) of the pre-oral part of the fore-gut is still very thick.

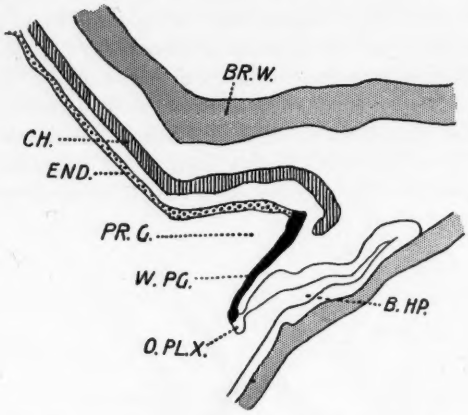


Text-fig. 23. R 210, 11 days, 37 somites. × 100.

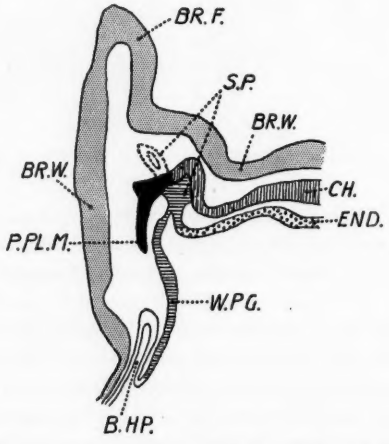
No definite trace of prochordal mesoderm was observed in any of the older embryos examined. Text-fig. 24 is a reconstructed median longitudinal section of an embryo decidedly older than the last one. No trace of the prochordal mesoderm was seen, and the chorda terminates in a recurved tip. Attention may be called to the curious flexures of the chorda seen in text-fig. 24 as well as in text-fig. 23. The latter is an actual tracing made from the median longitudinal section and the section on either side of it, so that in this embryo at all events the notochordal kinks are actually present as such. The hypophysis (*B.HP.*) is well developed but still open. The anterior wall of the pre-oral part of the fore-gut (*W.PG.*) is not thicker than the roof (*END.*).

After the above observations were completed, I examined a large number of embryos aged between 9 and 10 days. They support the conclusions set forth above. The last embryo examined showed a very well-developed Seessel's pouch, as seen in text-fig. 25. Here the chorda (*CH.*) ends as usual at this stage in the prochordal mesoderm (*P.PL.M.*). The very well-developed Seessel's pouch

marked ***S.P.*** arises from the dorsal angle of the fore-gut, and its distal end contains a closed cavity. It is asymmetrical and lies to the right of the middle line. It is clearly a derivative of the prochordal plate, since the wall of the fore-gut



Text-fig. 24. Part of reconstructed median longitudinal section of **R** 326, 11 days ¾ hour. × 100.



Text-fig. 25. Reconstructed median longitudinal section of anterior end of an embryo, 10 days, 26 somites. × 100.

from which it arises (the dorsal angle) is itself derived from that plate. This is the only case of its kind among the very numerous embryos I have examined.

Concerning the later history of the cranial end of the chorda, I may state that I have examined some forty embryos in order to try and determine the

relation of the tip of the chorda to the buccal hypophysis. The embryos range between 7 and 17·5 mm. in length, and in the later ones the chondrocranium is laid down. In thirty-nine embryos the tip of the chorda, although situated in the vicinity of the posterior wall of the buccal hypophysis, does not come in contact with it. In fact there is nearly always a capillary in contact with that wall. In the fortieth and last examined embryo (*Lepus*, 10 mm., *A.*), however, the tip of the chorda (actually its investing sheath) lay in close contact with the posterior wall of the buccal hypophysis. Reference may be made to the paper of Huber (11) in which this relationship is discussed.

SUMMARY

The preceding observations may be summarised as follows:

The prochordal plate is not the most anterior part of the embryonal endoderm, since in front of it the latter is thickened over a crescentic area (*P.END.*), the horns of which are continued backwards as lateral thickenings. In the thickened mesoderm overlying this area the pleuro-pericardial coelom is eventually developed. Its median anterior part contributes to the oral plate endoderm.

The prochordal plate (*P.PL.*) is at first a single-celled axial plate of thickened endoderm, and in the early stages there is no evidence of dorsal or lateral proliferation of cells from it. The plate is in continuity behind with the cranial segment of the head-process (*I.Z.*) which is not yet differentiated into typical chorda plate. As development progresses the prochordal plate shortens, and at the 3-somite stage it thickens dorsally and takes the form of a compact cellular mass several cells in thickness. It is distinctly separate from the limbs of the horseshoe-shaped endodermal thickening.

With the flexure of the brain and the formation of the fore-gut, the prochordal plate comes to form the cranial wall of the latter and probably also a very small part of the adjoining ventral wall.

At the 13-somite stage the chorda, up till now intercalated in the gut roof and in continuity at its anterior end with the prochordal plate, separates from the gut roof. A little later, in embryos of 14–15 somites, the prochordal mesoderm delaminates from the anterior wall of the gut, but its dorsal end remains in continuity with the chorda. The ventral part of the prochordal mesoderm is swollen cranial to the oral plate and has been homologised with the premandibular primordium or somitic mass, but no cavities were observed, except in one case, on one side only.

The chorda grows forward beyond its junction with the prochordal mesoderm as a free process in which mitotic figures are not infrequent. This relation explains the apparent bifid character of the anterior end of the chorda.

The prochordal plate derivatives comprise the anterior wall of the fore-gut, the prochordal mesoderm including the homologue of the premandibular somitic mass and probably a small part of the oral plate endoderm. Ultimately

the prochordal mesoderm is converted into mesenchyme. There is no evidence that the prochordal plate participates in the formation of the chorda.

DISCUSSION

The axial plate of endodermal cells, the history of which has been outlined here, has been designated differently by different observers. The name "prochordal plate" suggested by Van Oordt (18) seems to be the most suitable. It has been approved by Hill and Tribe (9), who have shown that this thickened patch of endoderm proliferates mesenchyme in the dog long before the primitive streak is laid down. This observation is of great value, since it shows that the prochordal plate cannot be of head-process origin. They also identified the prochordal plate in the early blastocysts of the cat. Van Beneden, in his posthumous paper of 1912 (5), also recognised the existence in the rabbit of a thickened patch of endoderm which was, however, one cell thick. He states that it indicates the bilateral symmetry of the embryo before the primitive streak makes its appearance. Whether this area is the prochordal plate or simply corresponds with the antero-median part of the horseshoe-shaped thickening, described here, it is not easy to decide, since he did not refer to it in his later stages. The same may be said of the thickened area described by Huber (10), who, however, denies the existence of the prochordal plate in the guinea-pig. Rabl (21) figured a similar area behind which, in older stages possessing a head-process, he figured a definite prochordal plate proliferating mesoderm from its dorsal surface, though he did not recognise it.

Hubrecht (12), however, was the first to distinguish a thickened patch of endoderm at the anterior end of the embryonal area in *Sorex* which he called the "protochordal plate" on the supposition that it contributes to the anterior end of the chorda. He recognised also another mesoderm-producing endodermal zone—his annular zone—the antero-median part of which constitutes the protochordal plate. Whether or not the horseshoe-shaped zone of thickened endoderm, described here in the rabbit, corresponds with the anterior part of Hubrecht's annular zone must remain an open question. This zone does not appear to give origin to mesoderm in the rabbit, and moreover the prochordal plate lies caudal to its antero-median part and in practically all the embryos is delimited from it. The general arrangement in the rabbit seems to resemble very much that in *Manis* described by Van Oordt (18), and his fig. 21 agrees with my text-fig. 1. According to Van Oordt's description and figures, however, his annular zone proliferates mesoderm like that of Hubrecht and eventually forms a complete ring by the junction of its lateral halves behind the primitive streak. The zone in question in the rabbit overlies the thickened band of mesoderm in which the pericephalic coelom arises, and a glance at text-figs. 1, 6 and 9 will convince one that the endothelial wall of the lateral heart tubes, which are the first constituents of the heart to be formed, cannot possibly be derived from the prochordal plate as suggested by Hubrecht (12,13). He also

derived the pharyngeal membrane and the wall of the fore-gut from the protochordal plate. It is, however, only the anterior wall of the fore-gut which is of prochordal origin, as the observations of K. M. Parker (19) and my own have shown.

Assheton (4) described in the rabbit an endodermal zone corresponding with the anterior part of Van Oordt's zone. He calls it the "pericardial thickening," but he does not describe any prochordal plate.

Bonnet (6) described a similar endodermal thickening which he called "Erganzungsplatte des Urdarmstranges"—the completion plate of the head-process. There is no justification for the name. He did not describe it in his youngest stages of the dog, though it appears quite early as Hill and Tribe have shown, but gave a detailed interesting account of it in later stages in which the primitive streak and the head-process were already established. He pointed out that it actively proliferates mesoderm and supports Hubrecht's view that it furnishes the anterior end of the chorda, but his argument is not convincing. The balance of opinion is against this view, and although I have shown that the prochordal plate shortens yet there is no evidence to show that that shortening is due to its conversion into head-process or chorda plate, rather is it to be regarded as the result of the considerable increase in thickness which it at the same time undergoes. Moreover the chorda grows forward in later stages beyond its point of contact with the prochordal mesoderm. As we are not examining the same embryo at different stages of its development but different embryos at different ages, it is quite possible that the apparent shortening may be due in part to individual variations in the degree of development of the plate.

Fig. 60 of Bonnet resembles my text-fig. 11. In his fig. 66, the chorda terminates in a mass of mesoderm proliferated from the anterior wall of the fore-gut. In principle, therefore, it resembles my text-fig. 15. Fig. 67 agrees with my Plate IV, fig. 23, which, however, exhibits no lateral extensions and a slender prochordal mesoderm.

K. M. Parker (19) has dealt in some detail with the prochordal plate in her paper on the hypophysis of the marsupials. There can be no doubt that her prechordal plate (Oppel (17)) is the equivalent of the prochordal mesoderm described here. Fig. 1 in her paper suggests that the prochordal plate gives rise to the anterior wall of the fore-gut as well as a part of the adjoining dorsal wall. She describes the termination of the chorda in the prechordal plate of mesoderm, but this plate lies more or less dorsal to the fore-gut, and in the stage figured blends by its apex with the anterior wall of the latter, whereas in the rabbit the prochordal mesoderm lies cranial to the anterior wall of the fore-gut. This difference, however, is purely topographical and is probably due to the more rapid brain development in the rabbit.

In the marsupials Miss Parker was able to trace the origin of the premandibular somites from the prechordal plate, whereas in the rabbit they do not apparently occur as definite structures, and all there is to represent them is

the ventral thickened part of the prochordal mesoderm—the premandibular somitic mass. Apart from these differences in detail our observations are in agreement.

Dorello (7), in reptiles, described a mass of endoderm in which the chorda terminates and which encloses the pre-oral gut. It gives rise to hollow buds—the head cavities. von Kupffer (15) found in *Bdellostoma* and *Petromyzon* that the chorda ends in a thickened endoderm in the wall of the pre-oral endoderm pocket.

Streeter (23) showed in the pig that the mesoderm grows forward in the form of two horns from the primitive streak region. They meet anteriorly, leaving a "bald" area in which the head-process makes its appearance before there is any sign of the prochordal plate. Soon the cells of the latter become piled on each other and show foldings which produce clefts that open into the fore-gut. He homologises this folded plate with the "Gaumentasche" described by Selenka in a much older stage of *Didelphys*. No such foldings are seen in the rabbit, and K. M. Parker ((19), p. 230) has suggested that the "Gaumentasche" "is nothing more than a prechordal plate in continuity with a well-developed Seessel's pocket."

Huber, Rabl, Kölliker and Keibel deny that the endoderm makes any contribution to the mesoderm. The thickened patch of endoderm recognised by Huber (10) in the guinea-pig is considered by that author as the primordium of the oral plate endoderm, in this respect agreeing with Keibel and Carius.

I have shown that the anterior end of the chorda does not come into direct contact with the buccal hypophysis, and that it is only the strand of prochordal mesoderm which, descending from its point of continuity with the chorda, terminates in the vicinity of the hypophyseal primordium. This is in agreement with Adelmann's statements (1,2) for the chick. He appears to think that in mammals the chorda very early acquires contact with the buccal hypophysis, but considers that the relation is a secondary one. He agrees with K. M. Parker that the premandibular somites are derived from the prechordal plate. His figs. 33–36 (2) closely agree with my text-figs. 15–23, but he does not describe any forward growth of the chorda beyond its contact with the prechordal plate. He points out that the brain grows more rapidly than the fore-gut and prechordal plate, thus leading to the formation of a mesenchyme-filled space in front of the prechordal plate and between it and the brain wall. On the whole my observations on the rabbit are in agreement with his based on the chick (2).

The chorda, in the stages examined, does not show any connection with the anterior wall of the fore-gut after its separation. In fact it grows forward beyond its union with the prochordal mesoderm. Grünwald and Staderini, however, have stated that the chorda comes into contact with Seessel's pocket. However that may be, the primary relation in the rabbit is that described above, namely, the termination of the chorda in the prochordal mesoderm.

Up to the stages examined there are no ventral extensions of the chorda connecting it with the dorsal wall of the fore-gut. Huber (11) described such

extensions in the human embryo and Grünwald in the sheep. These connections must clearly be secondary.

The apparent bifid anterior end of the chorda has already been explained. This condition has been figured by Grünwald (8), Keibel (14), Huber (11) and others, but in view of my observations, the contention that the chorda contributes to the hypophysis (Reichert, His and Dursy) must be regarded as very doubtful. In this connection, Kölliker described in an 11 day rabbit a strand of cells passing from the hypophysis to the chorda, and thought that it represented a contribution by the ectoderm to the chorda. It is clear that this strand is nothing but the remains of the prochordal mesoderm, as seen in Plate IV, figs. 28 and 29.

Saint-Remy (22) concludes that in all amniotes the anterior end of the chorda is bent down so that it can maintain its insertion into the epithelium of the buccal hypophysis. He states, moreover, that the descending limb is converted into connective tissue. In view of Adelmann's observations (1,2) on the chick and my own on the rabbit this statement must be regarded as incorrect so far as the insertion of the chorda is concerned. The descending limb referred to is not formed by chorda but by a prochordal mesodermal strand which is later transformed into mesenchyme, whilst the chorda can grow forward beyond it.

Keibel's figs. 38, 39, 40 *a*, 40 *b* (14) for the rabbit resemble my text-fig. 15, and his fig. 41 *b* seems to show an apparent bifid anterior end of the chorda, but the lower limb is very short and ends in the wall of the fore-gut in the region of Seessel's pocket. Paulisch's figs. 1, 2, 3 (20) of 9–11 days rabbits are very much like those of Keibel.

Atwell (3) figured a longitudinal section through the head of a 6 mm. rabbit embryo in which he showed an epithelial bud from the anterior wall of the fore-gut which more or less fuses with the tip of the chorda. He thinks it is identical with Selenka's "Gaumentasche" and Saint-Remy's descending branch of the chorda. It, no doubt, represents part of the prochordal mesoderm.

Some observers—von Kupffer, Saint-Remy and Miller (16)—hold the view that the anterior wall of the fore-gut contributes to the buccal hypophysis, but beyond the projections mentioned in the descriptive part of this paper I have no evidence that the anterior wall of the fore-gut contributes to the hypophysis in the rabbit.

I hope later to be able to examine rabbit embryos of 6 and 7 days and so complete this study of the history of the prochordal plate.

I wish to express my thanks to Mr A. K. Maxwell for touching up and lettering the text-figures and to Mr F. Pittock for the photomicrographs.

ABBREVIATIONS

B.HP.	Buccal hypophysis primordium.	*O.PL.X.*	Angle where ectoderm runs into endoderm.
BR.F.	Brain flexure.	*PAR.M.*	Paraxial mesoderm.
BR.PL.	Brain plate.	*P.END.*	Horseshoe-shaped or pericephalic zone of thickened endoderm.
BR.W.	Brain wall.	*P.PL.*	Prochordal plate.
C.FL.	Cephalic flexure.	*P.KT.*	Primitive knot.
CH.	Notochord.	*P.ST.*	Primitive streak.
CH.PL.	Chorda plate.	*P.COE.*	Pericephalic coelom.
CL.M.	Cloacal membrane.	*P.ST.M.*	Primitive streak mesoderm.
E.HT.	Endothelial heart tube.	*PP.C.*	Pericardio-peritoneal coelom.
END.	Endoderm.	*P.M.*	Pre-axial mesoderm.
FG.	Fore-gut.	*PC.C.*	Pericardial coelom.
F.FG.	Floor of fore-gut.	*P.PL.M.*	Prochordal mesoderm.
F.PC.C.	Floor of pericardial coelom.	*PR.G.*	Pre-oral part of fore-gut.
HF.B.	Head-fold bay.	*R.PC.C.*	Roof of pericardial coelom.
I.Z.	Cranial remains of head process.	*S.P.*	Seessel's pouch.
M.B.	Medial boundary of pericardio-peritoneal coelom.	*T.CH.*	Free tip of notochord.
M.S.	Mesodermal somite.	*W.PG.*	Anterior wall of pre-oral part of fore-gut.
O.PL.	Oral plate.		

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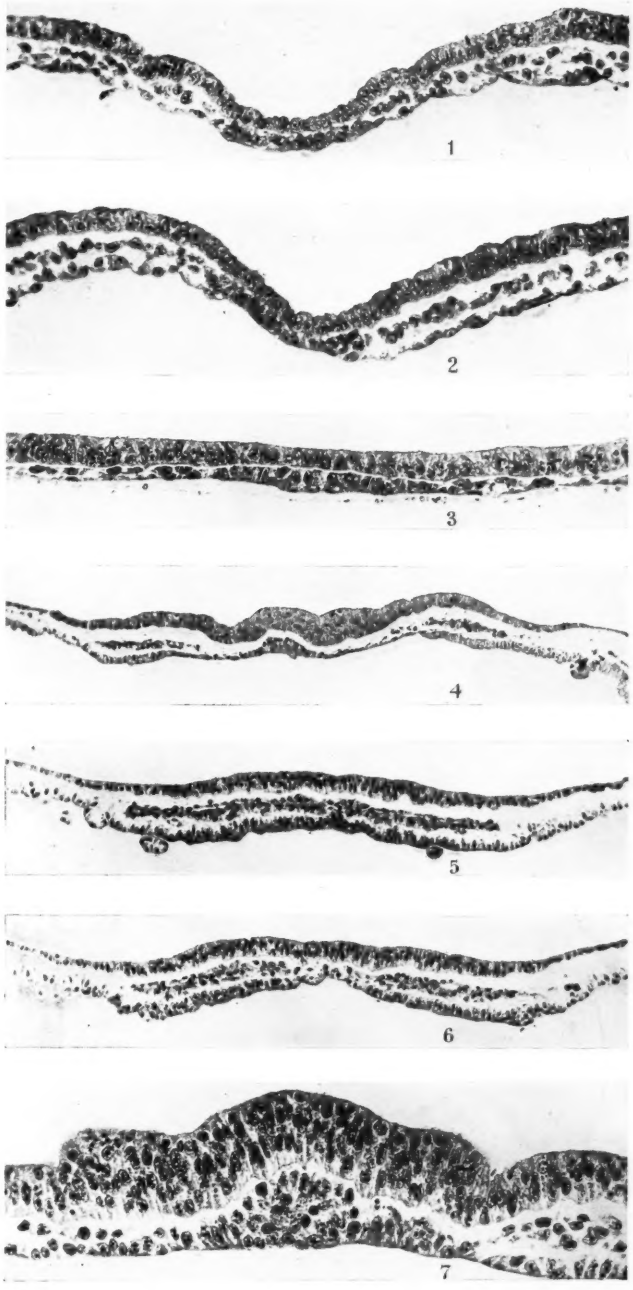

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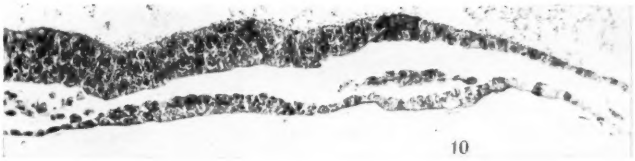

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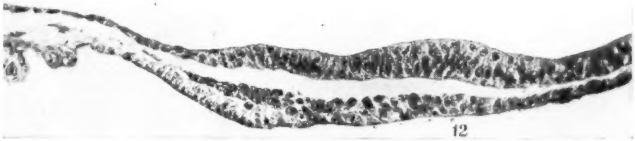

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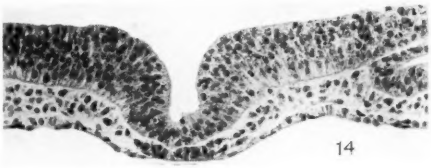
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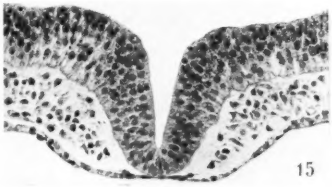
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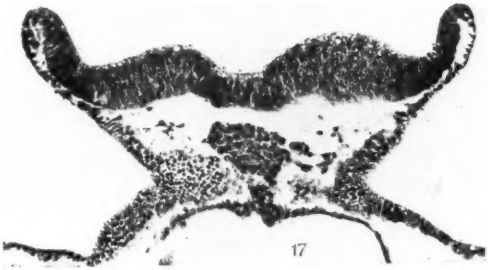
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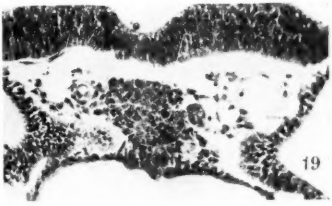
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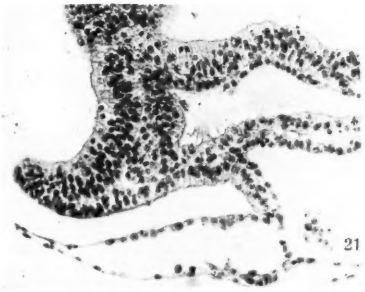
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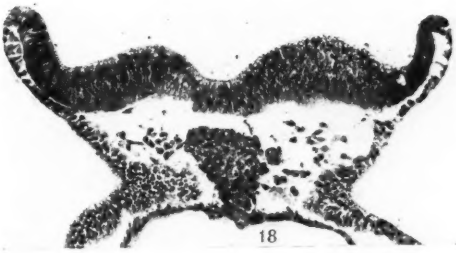
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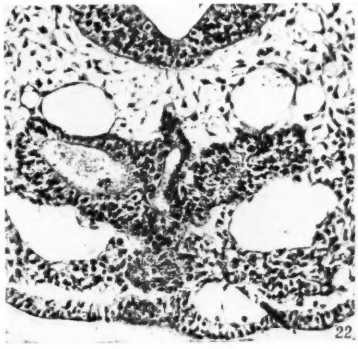
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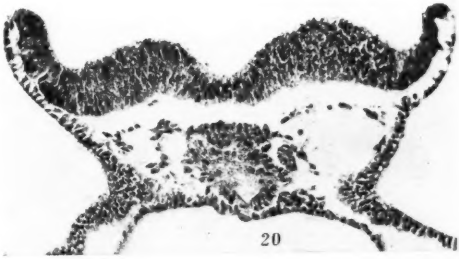
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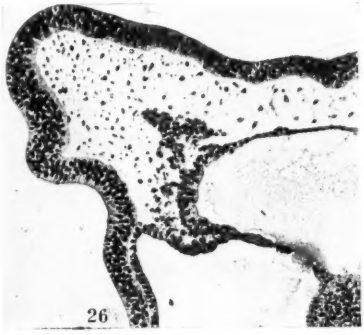

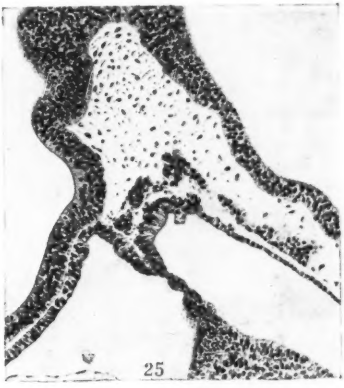

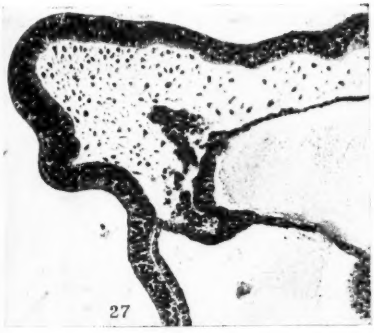

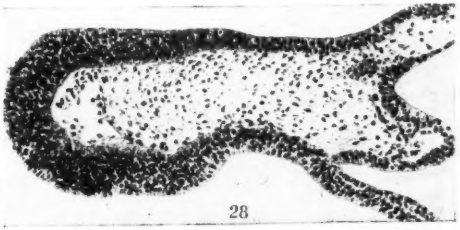

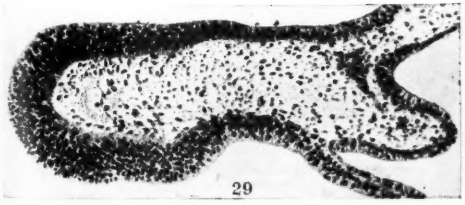

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EXPLANATION OF PLATES

The figures on Plates I and II have suffered a reduction of $\frac{1}{3}$, those on Plates III and IV a reduction of $\frac{1}{2}$.

Plate I

Fig. 1. T.S. (9.1.2.) of R 335, 8 days, primitive streak and head-process stage. × 330.
Fig. 2. T.S., 48th section behind fig. 1—same embryo as fig. 1. × 330.
Fig. 3. T.S. (4.2.2.) of R 352, 8 days 1 hour, ?1 somite. × 330.
Fig. 4. T.S. (25.1.2.) of rabbit *C*, 8 days, 3 somites. × 150.
Fig. 5. T.S., 22nd section of R 314, 8 days 17¾ hours, 4 somites. × 150.
Fig. 6. T.S., 28th section of same. × 150.
Fig. 7. T.S., 41st section of same. × 330.

Plate II

Fig. 8. T.S., 56th section of same as 5. × 330.
Fig. 9. T.S., 95th section of same as 5. × 330.
Fig. 10. Median longitudinal section (5.3.6.) of R 347, 8 days 3 hours, 5 somites. × 250.
Fig. 11. Longitudinal section (2.2.3.) of R 348, 8 days 3 hours, 5 somites. × 250.
Fig. 12. Median longitudinal section, 16th section after fig. 11, same embryo. × 250.
Fig. 13. T.S., 35th section of R 318A, 8 days 17¾ hours, 6 somites. × 250.

Plate III

Fig. 14. 50th section of same as 13. × 250.
Fig. 15. 67th section of same as 13. × 250.
Fig. 16. Median longitudinal section (6.4.5.) of R 359, 8 days 3 hours, 7 somites. × 250.
Fig. 17. T.S. (20.4.1.) of R 324, 8 days 17¾ hours, 8–9 somites. × 250.
Fig. 18. Next section of same. × 250.
Fig. 19. Next section behind 18 of same. × 250.
Fig. 20. Next section behind 19. × 250.
Fig. 21. Anterior part of a median longitudinal section (3.3.4.) of R 306, 8 days 16 hours, 9 somites. × 250.
Fig. 22. T.S. (18.5.1.) of R 179, 8 days 19 hours, 14–15 somites. × 250. Shows premandibular somitic mass.

Plate IV

Fig. 23. T.S. (8.3.2.) of R 253, 9 days 10 hours, 21 somites. × 250.
Fig. 24. 14th section behind 23. × 180.
Fig. 25. Median longitudinal section (6.3.2.) of R 248, 9 days 16 hours, 23–24 somites. × 180.
Fig. 26. Median longitudinal section (8.2.2.) of anterior part of R 255, 9 days 10 hours, 24 somites. × 180.
Fig. 27. Next section (9.2.2.) of same. × 180.
Fig. 28. Median longitudinal section (8.5.2.) of R 282, 10½ days, 30 somites. × 180.
Fig. 29. Section immediately after 28 (9.5.2.). × 180.
Fig. 30. Median longitudinal section (anterior part) (6.2.3.) of R 210, 11 days, 6·5 mm., 37 somites. × 135.

FURTHER NOTE ON THE PROCHORDAL PLATE IN MAN

By J. P. HILL and J. FLORIAN

From the Department of Anatomy and Embryology, University College, London

In our preliminary note entitled "The development of head-process and prochordal plate in Man" (this *Journal*, vol. LXV, part 2, January, 1931), we distinguished in the Dobbin embryo three portions in the axial formation situated in front of Hensen's knot, viz. a caudal portion, formed by a typical chorda canal, an intermediate portion in which the chorda process possesses three discontinuous lumina and is accompanied on both sides by lateral mesodermal bands, and a very short but broad cranial portion formed by a cellular mass, below which no independent layer of endoderm is distinguishable. This cranial portion we interpreted as a prochordal plate which had proliferated to form a mass of prochordal mesoderm. The object of this note is to state that we now regard that interpretation as erroneous.

Subsequent to the publication of our preliminary note, we have been able, through the kind permission of Prof. Dr F. Hochstetter, to study and to make photomicrographs of the prochordal plate—head-process region of the embryo Peh.$_1$-Hochstetter (Rossenbeck, 1923) which closely approximates to the Dobbin embryo in its stage of development. In the Peh.$_1$-Hochstetter embryo, the preservation of the cranial portion of the embryonal area is much better than in our embryo, and study of the sections has shown us that its prochordal plate bears no resemblance to our presumed prochordal plate in the Dobbin embryo, but has the form of a small thickened area of endoderm as described by Rossenbeck. In its thickest part the nuclei are arranged in two or three layers, whilst in its cranial part it consists of a single layer of cubical cells. The plate extends through seven sections, and is situated directly in front of what we regard as the anterior extremity of the head-process. In the Dobbin embryo we had observed a comparable area of thickened endoderm, which, however, was much less distinct than in the Peh.$_1$-Hochstetter embryo owing to the poor preservation of this region. The area in question is situated in front of, and extends back a short distance laterally to, our presumed prochordal plate. We had previously attached no special significance to this area, but we are now satisfied that its axial part at least corresponds to the prochordal plate in the Peh.$_1$-Hochstetter embryo, and that the mass which we interpreted in our preliminary note as formed by the prochordal plate and its mesoderm really represents the most cranial still undifferentiated portion of the head-process.

It is indicated in fig. 1 of our preliminary note as the coarsely dotted area situated close behind the anterior margin of the embryonal area. The area of thickened prochordal endoderm which lies immediately in front of, and laterally to, the dotted area is not indicated in the figure.

With that correction, the rest of the description given in our preliminary note of the preblastoporic axial structures in the Dobbin embryo holds good. These structures we now regard as comprising (1) the prochordal plate, relatively small and indistinct in the Dobbin embryo owing to the state of preservation and not yet in active proliferation; (2) the head-process, distinguishable into three parts, (*a*) a cranial short but broad segment as yet undifferentiated (the prochordal plate of our preliminary note), (*b*) an intermediate segment, in which the head-process is distinguishable into a median chorda process containing three isolated lumina of unequal length and two lateral mesodermal bands, (*c*) a caudal segment, in which the head-process has become transformed into a typical chorda canal provided with seven ventral openings into the yolk-sac cavity and a dorsal opening (blastopore, notopore) situated on Hensen's knot and leading into the amniotic cavity.

A detailed description of the Dobbin embryo, including a discussion of the development of the head-process and prochordal plate in early human embryos has been completed and will be published elsewhere[1].

[1] *Phil. Trans. Roy. Soc.* B. vol. 221.

PARTIAL DUPLICATION OF THE NOTOCHORD IN A HUMAN EMBRYO OF 11 MM. GREATEST LENGTH

By T. B. JOHNSTON

Guy's Hospital Medical School

The anomaly here recorded occurred in a human embryo of 11 mm. crown-rump length, which otherwise showed no gross abnormality. The embryo was cut in serial sections, 10 μ thick, and stained with haematoxylin and eosin.

The notochord was normal in extent, position and appearance, due allowance being made for the fact that the fixation of the specimen left a good deal to be desired. In the region of the second cervical ganglion, 70 μ caudal to

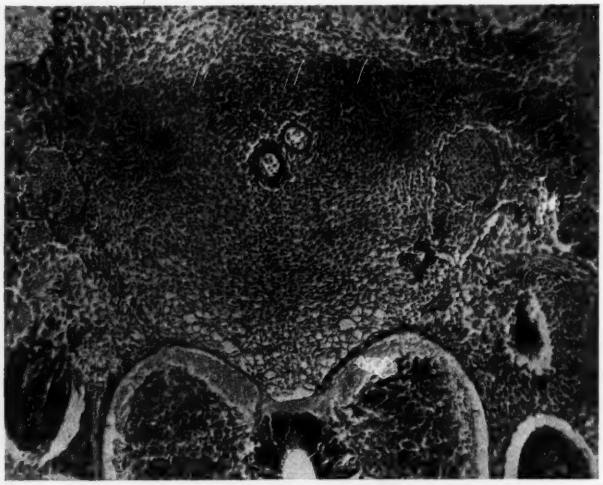

Fig. 1. The abnormal portion of notochord lies ventral and to the right of the normal portion. (Drawn by Mr J. E. Clapton from a microphotograph.)

the point where the notochord came into direct contact with the dorsal wall of the pharynx, a portion of a second notochord appeared, lying ventral and slightly to the right of the normal notochord. This abnormal portion extended only through four consecutive sections.

Thirty-three sections more caudally the abnormality reappeared. The abnormal portion of the notochord lay just ventral and to the right of the normal notochord and extended through six sections. In this situation the abnormal portion was very little smaller than the normal notochord (fig. 1), and it had no recognisable connection or attachment to it.

The significance of this rare anomaly (I have been unable to find any record of a precisely similar case) is not easy to determine, but it is important to observe that the normal notochord retained its median position throughout the whole of its extent. It may fairly be assumed that the notochordal plate in this embryo had been broader than normal in the upper cervical region, but there is no confirmatory evidence on this point in the floor plate of the spinal cord, which shows no widening nor any recognisable evidence of abnormal development. On this assumption, it would appear that the notochordal plate had given rise to two notochords in the upper cervical region, one of which retained continuity with the notochord in other regions, was dominant from the start and therefore occupied the median plane, while the other had been almost completely absorbed and only small portions of its cranial and caudal ends persisted in the specimen.

I was inclined at first to regard the two notochords as parallel (side-by-side) derivatives of the notochordal plate and to interpret the anomaly as an abortive and very imperfect attempt at twin formation. Another interpretation, however, is possible. During the process of excalation of the notochordal cells from the roof of the yolk sac, sufficient cells of the abnormally broad notochordal plate may have remained to constitute a second and more ventral notochord, which has been displaced from the median plane owing to the free character of its unattached extremities. Such a structure would be comparable to the hypochord, which is found as a transient structure in the embryonic stages of Selachians, Teleosts and Amphibia, but is unknown in Mammals.

GROWTH CHANGES IN THE BUSHMAN MANDIBLE

By LAWRENCE H. WELLS, M.Sc.

Department of Anatomy, University of the Witwatersrand, Johannesburg

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I. INTRODUCTION

The diagnostic characters of the adult mandible in both the Bushman and the Bantu have been fully described by Miss Salmons (1925). Subsequent investigations have merely served to confirm in detail the findings of this author.

The differences observed between the adult mandibles of the European, Bantu, and Bushman races naturally lead one to speculate as to how far these racial characteristics are present from birth, and to what extent they result from modifications in the process of growth. The present writer's interest in this problem was enhanced by the study of a fossilised fragment of the mandible of a child of about 5 years, discovered at depth in open country in the Zuurberg, some 50 miles north of Port Elizabeth in the Cape Province, which showed many differences from the mandibles of European children of this age (Wells, 1929). Prof. R. A. Dart had suggested to me that this fragment should be made the basis of a discussion of the growth changes in the mandibles of African races, but uncertainty as to whether the specimen should be referred to the Bushman or to some antecedent race, coupled with the shortage of suitable material for comparison, made me reluctant to undertake such a study.

Satisfactory material for the study of the growth changes in the Bushman mandible has, however, now become available. It forms part of a large collection of human skeletal remains obtained by Mr F. W. Fitzsimons, Director of the Port Elizabeth Museum, from an almost inaccessible cave in the Outeniqua Mountains. This range forms part of a series which runs parallel to the southern coast of South Africa, for a distance of 200 miles westward from Port Elizabeth. The mountains are situated some 12 miles from the coast, the intervening lowland belt being covered by the dense forests of Knysna and Zitzikama.

The coastal belt westward from Port Elizabeth forms, with the mountains behind, one of the richest archaeological provinces in South Africa, and it is especially noteworthy for the abundance in which it yields the skeletal remains of its former inhabitants. The finds made by Mr Fitzsimons in the caves of Zitzikama have formed the subject of no less than six papers (Dart, 1923; Laing, 1924, 1925; Gear, 1925, 1926; Laing and Gear, 1929), and to these must be added the Mistkraal (Allen, 1926) and Knysna (Fitzsimons, 1928) discoveries, as well as those made at the Zuurberg burial site on the extreme fringe of this area (Wells, 1929). The Outeniqua site was described by Mr Fitzsimons in 1926, and the human remains found, which form a valuable supplement to the discoveries already mentioned, will form the subject of a report by Mr J. H. Gear and the present writer. The work already done enables us to refer the skeletal remains to the Bushman race (broadly defined).

The specimens in the Outeniqua collection illustrating the development of the Bushman mandible are six in number. One is the right half of the mandible of a young infant; another that of a child of about 6 months. Another is the right half of the mandible of a child of 5–6 years, and is directly comparable with the Zuurberg fragment. Two are complete mandibles, aged 6–7 years and 9–10 years respectively, and the last consists of the greater part of the right half of a mandible aged 8–9 years.

In addition to these we have, besides the Zuurberg mandible, a fragment of a mandible aged about 5 years, not previously described, from a cave in the Zitzikama, and the mandible of a child of 8–9 years, found at Wepener in the Orange Free State. This last formed part of a skeleton loaned to us for examination by the Department of Bantu Studies of this University. On the basis of this material, a summary of which is given in Table I, it is possible to give an adequate account of the growth changes in the Bushman mandible.

Table I. *Juvenile Bushman mandibles*

Age	Description of specimen	Provenance
Infant	Right half of mandible	Outeniqua
6 months	„ „	„
5–6 years	„ „	„
5–6 years	Right ascending ramus and posterior part of body	Zitzikama
5–6 years	Symphysis and anterior part of body on both sides	Zuurberg
6–7 years	Complete mandible	Outeniqua
8–9 years	Right half of mandible	„
8–9 years	Complete mandible	Wepener
9–10 years	„ „	Outeniqua

The body of this paper falls naturally into two sections. In the first section will be given a description of the Bushman mandible at each of the stages at which we have specimens. In the second section comparisons will be drawn between the immature Bushman mandible and immature mandibles of other human races, both recent and fossil, as well as those of anthropoid apes.

II. THE AGE DIFFERENCES IN THE BUSHMAN MANDIBLE

(*a*) *Characters of the adult Bushman mandible*

The mandible of the adult Bushman, as described by Miss Salmons, has the following diagnostic features. The body of the mandible is short, but relatively high, and is much more robust than that of either the European or the Bantu. The mental protuberance is relatively slight, and there is little or no alveolar prognathism. The posterior surface of the symphysis faces somewhat upwards, but there is no true simian shelf. In nearly one-half of the specimens examined this surface bears genial fossae instead of genial spines. The ascending ramus is square, and set at right angles to the body. The sigmoid notch is shallow, and the postero-inferior angle is everted.

(*b*) *The mandible at birth*

The mandible of the Bushman infant (fig. 1 A) already displays the broad ascending ramus which is characteristic of the race. It is to be noted, however, that the ramus is set much more obliquely on the body than is the case in the adult. This obliquity of the ascending ramus is present to a nearly equal degree in the mandible of the European infant (fig. 1 B); in fact, it is an infantile character.

The postero-inferior angle, even at this early stage, is distinctly everted. The lower border of the body of the mandible is sinuous, showing three projections formed by the angle, by an elevation on the body in the region of the deciduous molars, and by the lower end of the symphysis. The sinuosity is much less marked in the European infant, in which neither the angle nor the lower end of the symphysis are so prominent.

In the region of the symphysis there is a considerable difference between the Bushman and the European mandibles. This is brought out in fig. 1 C, in which the outline of the European mandible (in broken line) is superimposed on that of the Bushman mandible (in continuous line). In the European infant the anterior surface of the symphysis is straight, and the mental portion projects somewhat in front of the alveolar portion. In the Bushman, on the other hand, the anterior surface of the symphysis is convex, and the mental portion recedes slightly behind the alveolar.

The mandible of the Bushman infant shows on its anterior surface near the symphysis the depressions described by Hrdlička (1930) under the name of *mental fossae*. There is also on the buccal aspect of the body of the mandible in its anterior portion a well-defined groove corresponding to the position of Meckel's cartilage in the foetus.

(*c*) *The mandible at* 6 *months*

A mandible at the stage just prior to the eruption of the central deciduous incisors is shown (somewhat restored) in fig. 1 D. In the formation of the ramus and body it is essentially identical with the mandible at the stage of birth. In the region of the symphysis, however, some differences are apparent. The anterior surface of the symphysis is less convex, owing to the modification of the alveolar region by the developing teeth, and to a change in the formation of the mental region, which now projects more forwards and less downwards, though it still recedes a little behind the alveolar portion. The mental fossae are still well developed, but the groove for Meckel's cartilage is almost completely obliterated.

(*d*) *The mandible at* 5–6 *years*

The form of the mandible immediately before the eruption of the first permanent molar tooth is shown by three specimens, from Outeniqua, Zitzikama, and the Zuurberg respectively. Of these, the Outeniqua and Zitzikama examples show the form of the ascending ramus, the Outeniqua and Zuurberg specimens that of the symphysial region, while the posterior portion of the body is preserved in all three. The corresponding parts of the three specimens agree in all respects except that of absolute size, so that a composite of the Zitzikama and Zuurberg fragments exactly reproduces the form of the more complete Outeniqua specimen. This last is represented in fig. 2 A.

The mandible at this stage is very massive in appearance. The broad ascending ramus is still obliquely placed, though less so than in the infant. The sigmoid notch is even shallower than in the adult.

The body of the mandible is much deeper near the symphysis than it is in the molar region. The inferior border is now concave, the elevation seen in earlier stages in the region of the deciduous molars having disappeared.

In the region of the symphysis a considerable change is apparent. The mental tubercles are now present in a rudimentary form, while the alveolar margin is prominent as a result of the eruption of the deciduous incisors. The anterior surface of the symphysis is now concave. In spite of the presence of mental tubercles, the chin recedes, the angle of the symphysis being 103°. The mental fossae have disappeared. The posterior surface of the symphysis faces somewhat upwards, and bears a deep genial fossa.

(*e*) *The mandible at* 6–7 *years*

This stage is represented in the Outeniqua series by a mandible in which the first permanent molar is fully erupted on the right side, and in process of eruption on the left (fig. 2 B). The mandible is now beginning to approximate to its adult appearance. The ascending ramus is somewhat oblique, but less so than in the preceding stage, and the sigmoid notch is deeper. The body is deeper anteriorly than posteriorly. The inferior border is concave in its posterior portion; anteriorly there is a slight projection below the first deciduous molar, which will be discussed in a later section (III (*d*)). The mental

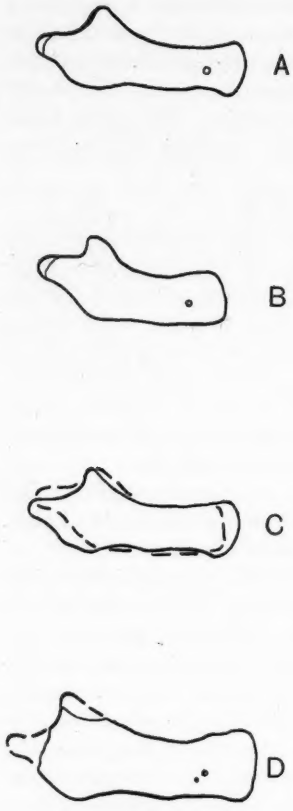

Fig 1.

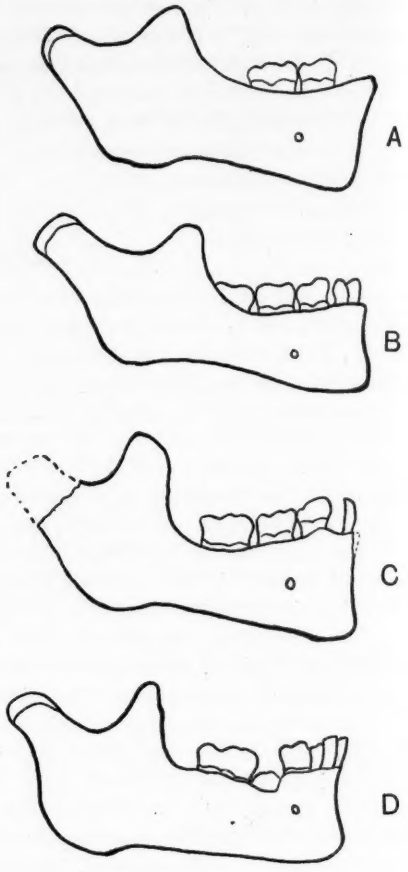

Fig. 2.

Fig. 1. A. Lateral aspect of mandible of a Bushman infant. B. Corresponding view of mandible of European infant. C. Outline of the European mandible (in broken line) superimposed on that of the Bushman mandible (in continuous line). D. Lateral aspect of mandible of Bushman child aged 6 months. × $\frac{2}{3}$.

Fig. 2. A. Lateral aspect of mandible of Bushman child aged 5–6 years. B. Lateral aspect of mandible of Bushman child aged 6–7 years. C. Lateral aspect of mandible of Bushman child aged 8–9 years. D. Lateral aspect of mandible of Bushman child aged 9–10 years. × $\frac{2}{3}$.

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tubercles have become much more prominent, so that the chin is no longer receding. A genial fossa is present.

(*f*) *The mandible at* 8–9 *years*

There is, as yet, in the collections of the University of the Witwatersrand no specimen of the Bushman mandible at the stage of eruption of the central permanent incisors. A fragment from Outeniqua and the mandible from Wepener correspond to the next stage, that of the eruption of the lateral permanent incisors.

The Outeniqua specimen (fig. 2 C) is the least complete of the mandibles from this site. It lacks the condylar process, and the alveolar margin is damaged at the symphysis. In this specimen the anterior border of the ramus is vertical, but the posterior is somewhat oblique. The body of the mandible is deeper anteriorly than posteriorly. The concavity of the inferior border, however, is less pronounced than in the preceding stage. The slight projection below the first deciduous molar is also seen in this specimen. The concavity of the anterior surface of the symphysis is almost abolished, possibly as a result of the eruption of the permanent incisors modifying the form of the alveolar margin. In consequence of this change the chin appears less prominent than in the preceding stage.

The Wepener mandible agrees exactly with the Outeniqua fragment in the formation of the symphysis. In the depth of the posterior portion of the body it approximates more closely to the adult condition, but in the slight obliquity of the ascending ramus it lags a trifle behind the Outeniqua specimen.

(*g*) *The mandible at* 9–10 *years*

This stage is represented in the Outeniqua series by a mandible in which the first premolar is fully erupted on the right side and in process of eruption on the left (fig. 2 D). The mandible has now attained the adult appearance in the following respects. The ramus is set at right angles to the body, and this, combined with the depth of the posterior portion of the body which equals that of the anterior portion, gives the characteristic square appearance to the mandible. The inferior border of the body is now straight, except for the projection of the postero-inferior angle. The projection of the mental tubercles is greater than in the preceding stages, so that the chin projects a little in front of the alveolar margin. A genial fossa is present.

(*h*) *Summary of the growth changes in the Bushman mandible*

In infancy the ascending ramus already shows the breadth characteristic of the mature Bushman mandible, but is much more obliquely placed than in the mature mandible. This obliquity is gradually reduced during growth, until the adult condition is reached by the 10th year. The sigmoid notch is shallower in early years than in the adult, attaining its adult condition by the 8th year. The eversion of the postero-inferior angle, seen in the adult, is already present in infancy.

The inferior border of the mandible is sinuous in early life. At 5–6 years it is concave, owing to the depth of the symphysis being greater than that of the molar region. This difference in depth has disappeared by 8–10 years, the inferior border becoming nearly straight.

At birth the anterior surface of the symphysis is convex, and the chin region is somewhat receding. By the 6th month the convexity is reduced, and at 5–6 years, as a result of the eruption of the deciduous incisors and the appearance of mental tubercles, the symphysis has become concave. The chin remains markedly receding until 6–7 years, when it becomes more prominent. The alveolar margin is further modified by the eruption of the permanent incisors (7–9 years). The region of the symphysis, like the ramus, has assumed the adult appearance by the 10th year.

The mental fossae of Hrdlička are present in early life, but have disappeared by the 5th year. The groove for Meckel's cartilage, which is present in infancy, has been almost wholly obliterated by the 6th month.

III. COMPARISON OF THE IMMATURE BUSHMAN MANDIBLE WITH OTHER IMMATURE MANDIBLES

(*a*) *Bantu mandibles*

The youngest specimen of a Bantu mandible in the collection of the Department of Anatomy is that of a child in which the second milk molar is erupting. This is unfortunately too damaged for detailed study.

In the mandible of a Bantu child of 3½ years (fig. 3 A) the ascending ramus retains the oblique infantile position, but is of the high narrow type with deep sigmoid notch, characteristic of the Bantu (Salmons, 1925). The inferior border of the body is concave, the body being deeper at the symphysis than in the molar region. The symphysis is slightly convex, and, although there is no indication of mental tubercles, the chin region is in the same vertical plane as the alveolar margin.

The further development of the Bantu mandible is illustrated by two specimens in which the lateral permanent incisors are erupted (8–9 years). The two mandibles are almost identical in appearance. One of them is illustrated in fig. 4 A, and in fig. 4 B the same specimen is compared with the Outeniqua Bushman mandible of corresponding age, the Bantu mandible being shown in full line, the Bushman in broken line. Apart from the difference in absolute size, the Bantu mandible may be distinguished from the Bushman mandible by the high narrow ramus, more massive chin, and more pronounced alveolar prognathism, which are its diagnostic racial characters (Salmons, 1925). In the direction of the ramus, the depth of the posterior portion of the body, and the form of the symphysial region, the Bantu mandible agrees with the adult type, i.e. the Bantu mandible has assumed its adult characters at 8–9 years, which is rather earlier than in the Bushman.

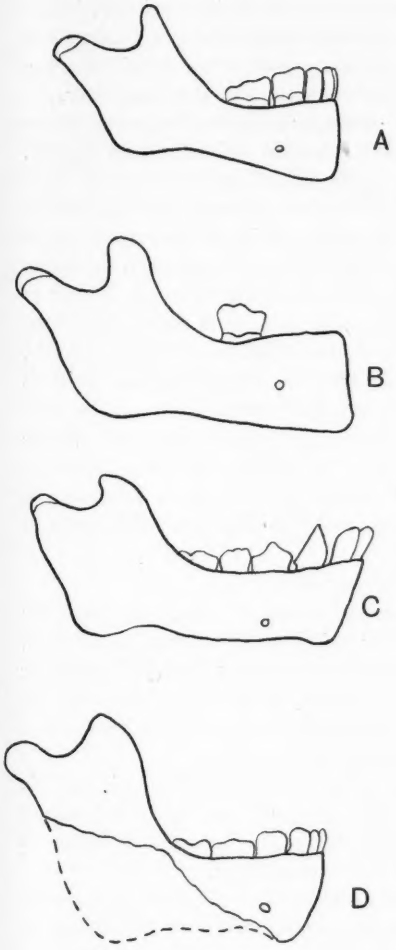

Fig. 3.

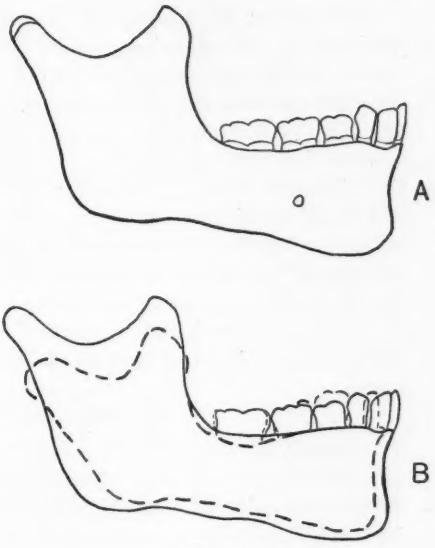

Fig. 4.

Fig. 3. A. Mandible of Bantu child aged 3½ years. B. Mandible of European child aged 5 years. C. Mandible of young chimpanzee (first molar erupting). D. Mandible of *Australopithecus* (restored portion indicated in broken line). × ⅔.

Fig. 4. A. Mandible of Bantu child aged 8–9 years. B. Mandible of Bantu child aged 8–9 years (in continuous line) compared with the mandible of a Bushman child of the same age (in broken line), superimposed on the alveolar plane, first permanent molars in coincidence. × ⅔.

(*b*) *European mandibles*

The mandibles of the European infant and that of the Bushman infant have already been compared (fig. 1 C). The principal differences between them are in the breadth of the ascending ramus, the contour of the inferior border, and the direction and curvature of the anterior surface of the symphysis. In the European infant the ramus is narrow, the inferior border is convex rather than sinuous, the symphysis is straight and the mental region projects slightly.

The further development of the European mandible is shown by three specimens in our collection all aged between 4 and 6 years. One of these is represented in fig. 3 B, and in fig. 5 A the same specimen is compared with the Bushman mandible of the same age, the European being shown in broken line and the Bushman in continuous line. The European is much lighter in construction than the Bushman mandible, with a narrow ramus and deep sigmoid notch. The body is as deep in the molar region as at the symphysis. The most conspicuous difference, however, is in the mental region, which is salient in the European whereas it is receding in the Bushman. The prominence of the chin in the European is due in part to the difference in the direction of the symphysis already present in the infant, but it is accentuated by the more precocious development of the mental tubercles, which are as well developed in the European at 5 years as in the Bushman at 8 years or more.

(*c*) *The mandible of La Genière*

Gaillard, Pissot, and Cote (1927) have described the skull and mandible of a child of 6–7 years from the Late Magdelenian rock-shelter of La Genière, Serrières-sur-Ain, France. This individual they regard as "negroid" and refer to the Grimaldi race. In view of the supposed Bushman affinities of the Grimaldi skeletons, it is of interest to compare the mandible of La Genière with immature Bushman and Bantu mandibles.

Unfortunately we have no specimen of precisely the same age as this individual. We have, however, both slightly older and slightly younger Bushman mandibles, so that a fairly accurate comparison with this race is possible, and we also have slightly older Bantu mandibles.

The authors describe the mandible of La Genière in the following terms: "Examinés de profil, les branches montantes sont obliques et de faible largeur. Le corps de la mandibule, assez grêle au niveau de la première molaire, est plus robuste dans la région antérieure. Le menton est droit." In addition to these points, the authors' figure shows that the posterior border of the ramus is more nearly vertical than the anterior, so that the ramus is broader below than above.

In the region of the symphysis the mandible of La Genière appears not dissimilar to the slightly older Bushman mandible from Outeniqua, though the mental tubercles appear to be even less prominent than in the Bushman. The ramus, however, is quite different from that of the Bushman mandible

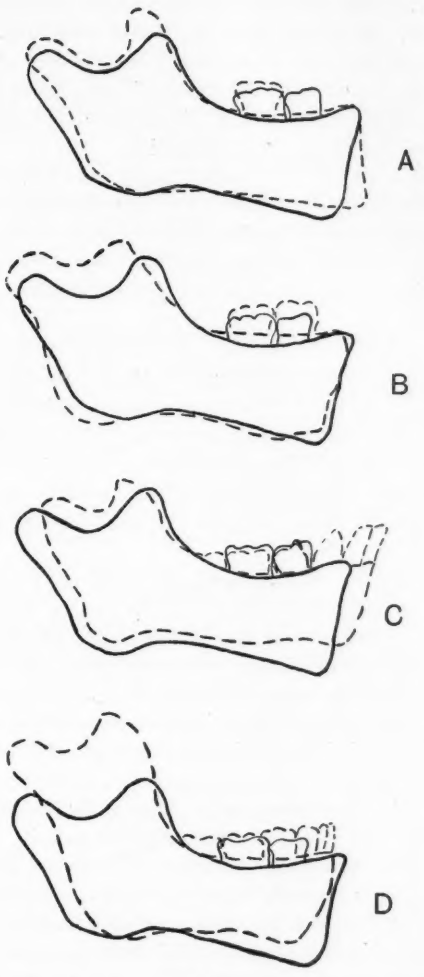

Fig. 5. The mandible of a Bushman child aged 5–6 years compared with A, the mandible of a European child aged 5 years; B, the mandible of a Neanderthal child aged 5 years; C, the mandible of a chimpanzee in which the first molar is erupting; D, the mandible of *Australopithecus*. The Bushman mandible is shown in continuous line in all cases. (Superimposed on the alveolar plane, second deciduous molars in coincidence.) × ⅔.

at any age, and is by itself quite sufficient to preclude the possibility of any close relationship of this individual to the Bushman.

In the form of the ramus the mandible of La Genière presents greater, but by no means close, resemblances to the Bantu mandible. The form of the symphysis, however, is by no means such as one would infer from the available evidence to be present in the Bantu at this age. There is thus no evidence to be drawn from the structure of the mandible in favour of the supposed African affinities of the La Genière-Grimaldi race.

Gaillard, Pissot, and Cote themselves point out that the dentition of the La Genière individual presents many features of affinity with that of the Australian aboriginal. There is thus more valid evidence for regarding the La Genière skull as "Australoid" than as "Negroid," and this is in accordance with the observation of Elliot Smith (1927) upon the Grimaldi remains.

(*d*) *The mandible of the Devil's Tower*

Miss Salmons expresses the opinion that the Bushman mandible is in many respects "more comparable with the more primitive types of mandible, e.g. the Neanderthal or Heidelberg mandibles, than it is with the European or the Bantu type." It is therefore of especial interest to compare the Bushman mandible of 5–6 years with the Neanderthal mandible of corresponding age from the Devil's Tower, Gibraltar (Garrod, Buxton, Elliot Smith and Bate, 1928).

The two mandibles are shown in super-position in fig. 5 B, the Bushman being in full line and the Neanderthal in broken line. The Neanderthal mandible is even more massive than that of the Bushman. The ascending ramus is high, and is further distinguished by the posterior border being more nearly vertical than the anterior, somewhat as in the La Genière mandible. In consequence, the postero-inferior angle is more salient than in the Bushman, and, further, this angle is inverted in the Neanderthal mandible, whereas it is everted in the Bushman.

The form of the inferior border in the Neanderthal mandible is very similar to that of the Bushman mandible, except in its anterior portion, where the Neanderthal specimen shows a prominence which is not seen in the Bushman at this age, though it is present, to a less pronounced degree, at a later stage in development (fig. 2 B and C). Buxton states that in the European this tubercle is seen only in the mandibles of muscular adults. It is suggested that it may serve for the attachment of the platysma muscle. Its presence in a reduced condition in the Bushman may be regarded as a Neanderthaloid feature.

The symphysis of the Bushman mandible at this stage resembles that of the Neanderthal mandible more closely than any other. The chin recedes a little more in the Neanderthal than in the Bushman child, the angle of the symphysis being 103° in the Bushman and 106° in the Neanderthal mandible. The difference is due to the somewhat greater development of the mental

tubercles in the Bushman, which imparts to the Bushman symphysis the concave contour which is not seen in the Neanderthal child.

It appears from this comparison that the immature Bushman mandible is in many respects intermediate in structure between the Neanderthal and the European type. This conclusion is in accordance with the observations of Miss Salmons, and also with observations on other portions of the Bushman skeleton which frequently reveal Neanderthal-like features[1].

(*e*) *Chimpanzee mandibles*

This Department possesses five mandibles of immature chimpanzees. Of these one is at the stage immediately preceding the eruption of the first permanent molar, in two others that molar is in course of eruption, and in the remaining two it is fully erupted.

Fig. 6. Mandible of a chimpanzee in which the first molar is unerupted (in continuous line) compared with that of a Bushman at the same stage of development (in broken line). × $\frac{2}{3}$.

In fig. 6 the mandible of the chimpanzee in which the first molar is unerupted is shown in continuous line, and the Bushman mandible of the same stage of development is superposed on it in broken line. The mandible of the chimpanzee is lighter in construction than that of the Bushman. In its form it resembles the mandible of the Bushman infant more than any later stage in development. It displays the same very oblique ascending ramus, the same sinuous contour of the lower border of the body, and the same boldly convex and markedly receding symphysis, all of which features have been lost in the Bushman mandible at the corresponding stage of development.

A chimpanzee mandible in which the first molar is erupting is represented in fig. 3 C, and in fig. 5 C the same specimen (in broken line) is compared with the 5-year-old Bushman mandible (in continuous line). The chimpanzee mandible has undergone considerable changes, but largely in a direction different from that of the growth changes in Man. The ascending ramus is slightly less oblique than in the earlier stage. The body has become considerably elongated as a result of the increasing prognathism, and its lower border is still decidedly sinuous. The symphysis is still markedly receding, but instead of being convex it is now almost straight. The incisor teeth are somewhat procumbent. In the older chimpanzee mandibles these modifications are still further exaggerated.

[1] See, in addition to articles cited in this paper, Wells, "The Foot of the South African Native," *Am. J. Phys. Anthrop.* vol. xv, pt II, and Shore, "Cervical Spinous Processes in Native Races of South Africa," *J. Anat.* 1931, vol. LXV, p. 482.

(*f*) *The mandible of* Australopithecus

The mandible of the type of *Australopithecus africanus* Dart (an immature individual in which the first permanent molar is in process of eruption) is shown in fig. 3 D, the restored portion being indicated in broken line. In fig. 5 D the restored mandible (in broken line) is compared with the 5-year-old Bushman mandible (in full line). It will be seen that the body of the *Australopithecus* mandible is relatively short, while the ascending ramus is narrow and unusually high. These features imply a small degree of prognathism combined with marked "subgnathism." The chin is receding, and the symphysis is notably convex, as in the chimpanzee at a slightly earlier stage, in the Bushman infant and in the immature *Sinanthropus* (Black, 1929).

This is not the place to enlarge upon the many differences between the mandible and teeth of *Australopithecus* and those of the chimpanzee, as this has already been done by Dart (1929). The fact that the *Australopithecus* mandible is best compared with younger chimpanzee mandibles and with those of primitive human infants deserves emphasis, however, for it suggests that *Australopithecus* is near to the stem form from which these divergently specialised groups arose. Further, it may be noted that the mandible of *Australopithecus* also has affinities with those of *Propliopithecus* on the one hand, and of *Eoanthropus* and of *Sinanthropus* on the other.

IV. SUMMARY AND CONCLUSIONS

1. The ascending ramus of the Bushman mandible already shows its characteristic breadth and the eversion of the inferior angle in infancy. The ramus is at first obliquely placed, but by the 10th year it is set at right angles to the body.

The inferior border of the body is sinuous in early life. By the 5th year it is concave, and at the 10th year has become nearly straight. The mental region is receding at birth, and remains so until the 5th year, when it becomes more prominent. The adult condition of the symphysis is attained at about 9–10 years. Mental fossae are present in early life, but have disappeared by the 5th year.

The mandible has attained the adult appearance by the 10th year.

2. The differentiating characters of the Bantu mandible are present from an early age. The mandible has assumed its adult form by about the 8th year.

3. The direction of the symphysis menti in infancy is different in the Bushman and in the European. The mental tubercles also develop more precociously in the European than in the Bushman.

4. The mandible of La Genière shows no features of affinity with the immature Bushman mandible. It therefore offers no support to the suggestion that the La Genière-Grimaldi race is related to the Bushman.

5. The Bushman mandible at the 5th year is intermediate in its features

between the European and the Neanderthal mandibles at the same age, but resembles the Neanderthal type more closely than the European.

6. The mandibles of the juvenile chimpanzee and of *Australopithecus* present many features of affinity with the mandible of the Bushman infant.

In conclusion, I have to express my thanks to the Port Elizabeth Museum and the Department of Bantu Studies for the loan of specimens, and to Dr L. R. Shore for his kind advice during the preparation of this paper.

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CRANIO-CLEIDO DYSOSTOSIS AND NORMAL SKULL FORMATION

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When studying the register of measurements of 1896 medical students, made under my supervision in the Anthropometric Laboratory of the Department of Anatomy of the University of Aberdeen, the idea suggested itself that there might be some statistical correlation between the breadth of the shoulders (biacromial breadth), which is mainly accounted for by the lengths of the clavicles, and the shape of the skull.

The idea originated from the fact that there seemed to be a direct relation between the development of the clavicles (fundamentally ossified in membrane or for the most part in membrane and partly in cartilage) and that of the bones of the cranium and face (essentially developed in membrane) in bringing about the rare congenital condition of cranio-cleido dysostosis.

In spite of the fact that, although made by expert anatomists working in a laboratory devoted to anthropometric research, biacromial measurement of the living body is often unsatisfactory and liable to a certain amount of error, statistics were taken from the register of 800 male medical students of an average age of 22 years as regards biacromial breadth, cranial length and cranial breadth, face length and face breadth, in order to find out if, by statistical examination, any correlation existed between biacromial breadth and shape of skull.

From the data supplied tables were constructed in order to determine the means and standard deviations of biacromial breadth, cranial length, cranial breadth, face length and face breadth, with the result as shown in Table I.

Table I.

	Mean (mm.)	Error (mm.)	Standard deviation	Error
Biacromial breadth	384·16	±·527	22·11	±·373
Cranial length	195·65	±·1404	6·024	±·0995
Cranial breadth	153·712	±·1245	5·22	±·088
Face length	123·418	±·153	6·4	±·01
Face breadth	136·64	±·14	5·91	±·0024

Correlation tables were then made out as regards biacromial breadth and cranial breadth, biacromial breadth and cranial length, biacromial breadth and face length, biacromial breadth and face breadth, and from these correlation coefficients were obtained as shown in Table II.

Table II.

	Correlation coefficient
Biacromial breadth and cranial breadth	−·0443
Biacromial breadth and cranial length	+·00425
Biacromial breadth and face length	−·00685
Biacromial breadth and face breadth	+·0687

It will thus be seen that, from the material supplied, which is preserved in the Anatomy Department of the University of Aberdeen and may be consulted by any interested, the investigation shows that there is practically no correlation between breadth of shoulders (biacromial breadth) and shape of head in normal male individuals.

Although the surmise that some relation might exist between breadth of shoulders and shape of head in normal male individuals, the above research has proved it to be anthropometrically erroneous, yet a record of the investigation may be of interest and worthy of note.

I am indebted to Prof. A. Low for the use of the Anthropometric Register and to Mr J. D. Macdonald, B.Sc., for his help in the research.

THE INTRAPONTINE PART OF THE MOTOR ROOT OF THE FACIAL NERVE

By E. VERNON, B.Sc.

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INTRODUCTION

Although the petrous and peripheral parts of the facial nerve are known in considerable detail, it is not uncommon to find conflicting statements regarding the intrapontine part of this nerve. Dr E. R. A. Cooper, of Manchester University, suggested to me that this problem might be investigated by gross dissection. Where possible, dissections in the solid have a marked advantage over histological sections, particularly in a case such as this, where a three-dimensional object is to be traced.

On preparing a number of such dissections, it became apparent that the intrapontine root of the VIIth nerve showed four flexures, dividing the root into five distinct parts, instead of the three parts allotted to it by most writers. Moreover, these individual parts bore relations to neighbouring structures in the pons, which were apparently dependent on the developmental history of the nerve.

METHOD OF PREPARING THE DISSECTIONS

This account is based on observations made on fifteen dissections of adult human brain stems. Only one side of each was dissected, left and right sides being chosen alternately. It was found necessary to work in a strong, direct light, so arranged as to play along the length of the fibres of the nerve bundle. By this method, no difficulty was experienced in recognising and tracing the nerve amongst the surrounding white fibres.

After consideration of several preliminary dissections, the following method of approach was decided upon:

Two fixed points were taken, viz. the superficial origin of the facial nerve, and the depression marking the junction of the superior and middle cerebellar peduncles (*X* in fig. 1). The knife was introduced into the combined mass of the middle and inferior cerebellar peduncles, and a parasagittal incision made, down to the level of the line joining these two points. (It will be seen that a part of the intrapontine root of the VIIth nerve lies along this line.)

The middle peduncle was then shaved off at right angles to this incision, until the level of the ingoing Vth nerve was reached. This nerve, when traced to its pontine nucleus acted as a guide to the position of the VIIth nerve, which passes medial to the spinal tract of the trigeminal. The facial nerve was then followed from its superficial origin, along the angle between the two cut surfaces (fig. 2).

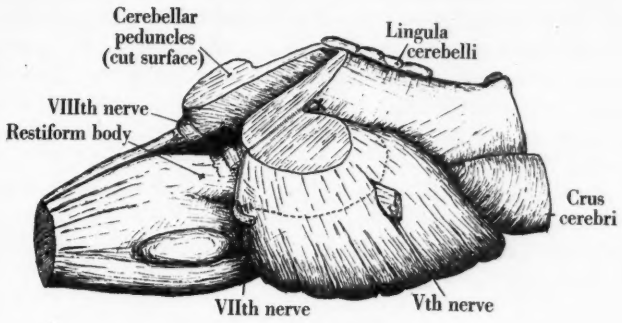


Fig. 1.

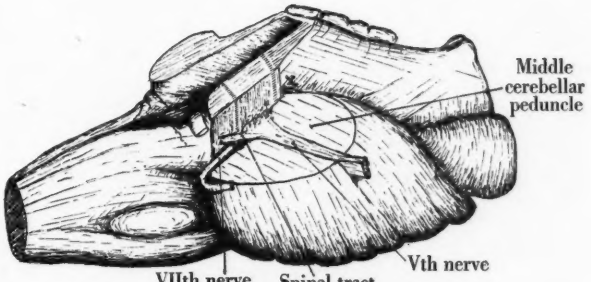


Fig. 2.

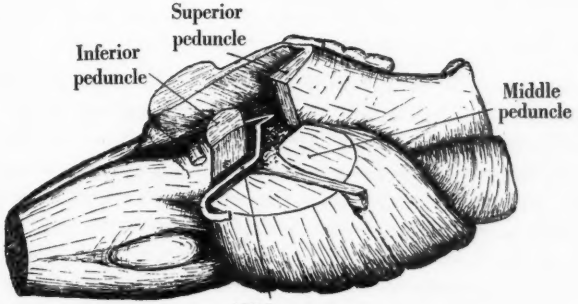


Fig. 3.

At this point, it was found more convenient to turn to that part of the root of the VIIth nerve lying in the floor of the IVth ventricle. The genu of the root was first isolated at the cephalic end of the facial eminence by stripping away the overlying ependyma. From this point the "second" part, or ascending portion of the root, was traced caudally, until, just cephalic to the striae acusticae, it sank deeply into the tegmentum of the pons, as the "first" part.

Again, from the genu the emerging root was traced across the floor of the ventricle to the fovea superior. The superior and inferior cerebellar peduncles were then separated, and sufficient cut off each to allow the two parts, so far disclosed, to be connected up (fig. 3).

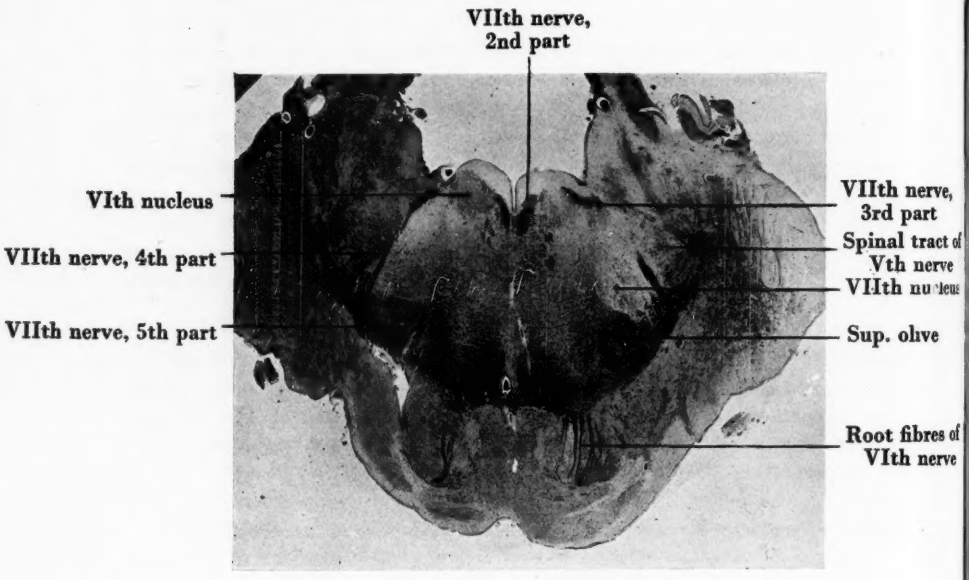


Fig. 4. Caudal border of pons. Section A 69. Low power.

With the exception of the nucleus and the first part, the whole of the intrapontine course of the facial root was now exposed.

In order to study the nucleus of origin and the first part of the root of the VIIth nerve, and also to observe the relations of the emerging facial root to the neighbouring pontine nuclei, the dissections were supplemented by two series of histological sections, cut from full-term foetal brain stems. An interval of 80 microns was allowed between consecutive sections. The stain used was Loyez's haematoxylin, which stains both myelinated fibres and nerve cells a dense blue-black. For the purposes of this investigation the additional cellular stain gave a decided advantage over the Weigert-Pal method (fig. 4).

In the following account, the intrapontine course of the facial root will be divided into the five parts observed. The nucleus of origin and also the first two parts are already well known, but, nevertheless, a brief account of these portions will be given for the sake of continuity.

DESCRIPTION OF THE COURSE IN THE PONS

(1) *The nucleus of origin*

The motor nucleus of origin of the VIIth nerve consisted of an ovoid group of large, multipolar nerve cells, arranged in four subgroups, viz. a dorsal, intermediate, ventral, and medial group. The nucleus was situated deeply in the reticular formation of the caudal end of the pons, just medial to the spinal tract of the Vth nerve and its own emergent root, and dorsal to the superior olive (fig. 4).

(2) *The first part of the root*

This part of the root emerged from the dorso-medial aspect of the nucleus as a diffuse stream of fibres which ran dorso-medially towards the floor of the IVth ventricle. On arriving ventral to the VIth nucleus, the fibres turned directly medially, some of the more caudal fibres passing through the nucleus, to reach its medial aspect. The fibres from the most caudal portion of the nucleus reached the floor of the ventricle just cephalic to the striae acusticae.

(3) *The second part of the root*

Having reached the medial side of the VIth nucleus, the fibres of the facial root now turned abruptly cephalically, thus forming a compact, rounded bundle (known by some writers as fasciculus teres). This bundle lay just medial to the VIth nucleus and dorsal to the posterior longitudinal bundle. Fibres of the first part of the root, from the more cephalic portions of the VIIth nucleus, entered along the ventral aspect of the second part, as it ascended. This second part was 5–6 mm. in length and terminated by an abrupt flexure which formed the genu of the root (fig. 5).

(4) *The genu of the root* (*Genu internum*)

Having ascended to the cephalic end of the VIth nucleus, the emerging root of the facial nerve turned abruptly laterally and caudally, passing dorsally over the much-reduced, cephalic end of the VIth nucleus. This lateral bend caused an angle of 65° between the second and third parts of the root.

It should be noted that it is in the description of the succeeding parts of the facial root that most discrepancies are found in the current accounts. Many writers state that from here the facial root passes straight to its superficial origin in a ventro-caudal direction, piercing the whole thickness of the pontine fibres.

In these dissections this was found not to be so. The nerve bundle pursued a devious but definite course with regard to its neighbouring structures, as follows.

(5) *The third part of the root*

From the genu, the emerging nerve bundle turned laterally and caudally across the floor of the ventricle. After a course of 4 mm. in this direction the facial root reached the fovea superior, where it left the floor of the ventricle (fig. 5).

In transverse sections, this part was seen as an obliquely cut bundle, lying to the lateral side of the prominent VIth nucleus (fig. 4).

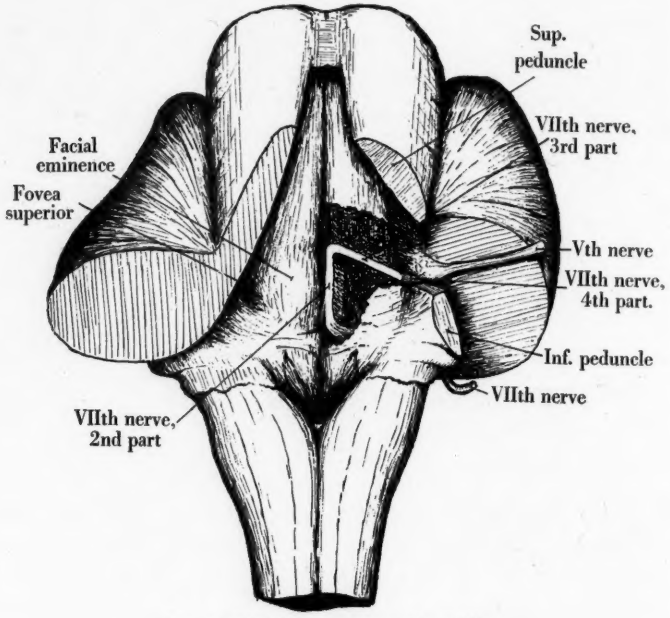


Fig. 5. Dissection seen from dorsal side.

(6) *The fourth part of the root*

At the fovea superior, the nerve bundle left the floor of the ventricle by passing through a roughly triangular interval in its wall. This interval was produced at this point by the restiform body, which forms the lateral wall of the ventricle in its more caudal portion, turning dorsally to become the inferior cerebellar peduncle. Thus, in passing through this exit, the facial root lay ventro-caudal to the superior cerebellar peduncle, and ventro-cephalic to the commencement of the inferior cerebellar peduncle.

At this point, the emergent root turned ventrally and laterally and sank through the reticular formation, medial to the middle cerebellar peduncle. Towards the end of this part, the root passed between the spinal tract of the Vth nerve laterally, and its own nucleus of origin medially. Immediately after passing these two structures, the facial root met the mass of the middle cerebellar peduncle and in consequence suffered a further change of direction. The length of this part of the nerve averaged 4 mm. (fig. 6).

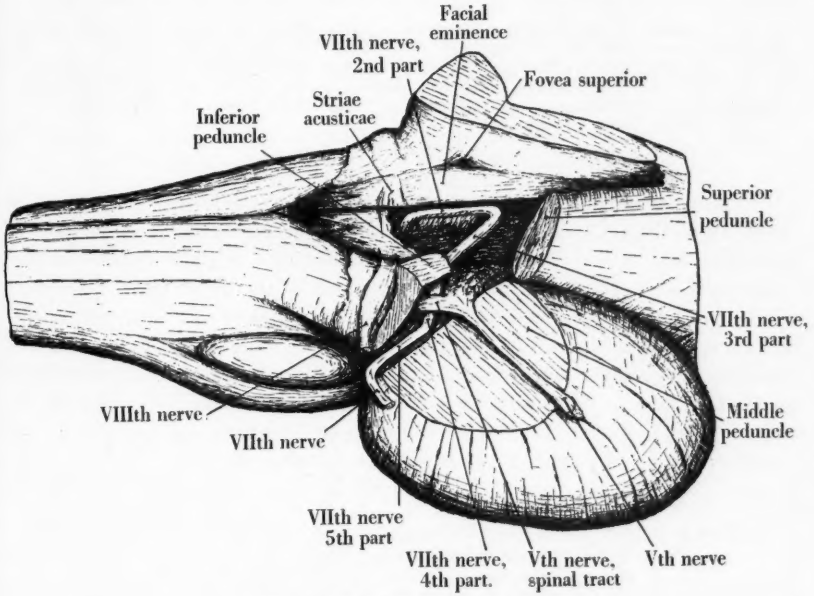


Fig. 6. Dissection seen from right side.

(The constancy with which the emergent facial root took the fovea superior as its guide to the exit from the floor of the ventricle suggested that the fovea arose as a "dimple" in the ventricular ependyma, pushed into the deficiency in its lateral wall, caused by the dorsal turn of the restiform body, as it becomes the inferior peduncle of the cerebellum.)

(7) *The fifth part of the root*

Further progress in a ventro-lateral direction being prevented by the body of the middle peduncle, the facial root now turned in a ventro-caudal direction and pursued a course between the middle peduncle and the restiform body. The VIIth root ran in this direction for a distance of 5 mm., lying dorso-medial to the middle peduncle and ventral to the restiform body, until it reached its superficial origin on the ventro-lateral aspect of the brain stem (fig. 6).

Tabulated summary of course

First part	Second part	Third part	Fourth part	Fifth part
Direction				
Dorsally and medially at 45° to the sagittal plane	Cephalically	Caudally and laterally at 65° to the median sulcus of the ventricle	Ventrally and laterally at 30° to the sagittal plane	Caudally and ventrally at 45° to the horizontal plane
Length				
From the nucleus of the VIIth nerve to the medial side of the VIth nucleus, 4 mm.	From the medial side, to the cephalic end of the VIth nucleus, 5–6 mm.	From the cephalic end of the VIth nucleus, to the fovea superior, 4 mm.	From the fovea superior to the ventral border of the VIIth nucleus, 4 mm.	From the ventral border of the VIIth nucleus, to the superficial origin, 5 mm.

ADDITIONAL FIBRES IN THE FACIAL NERVE

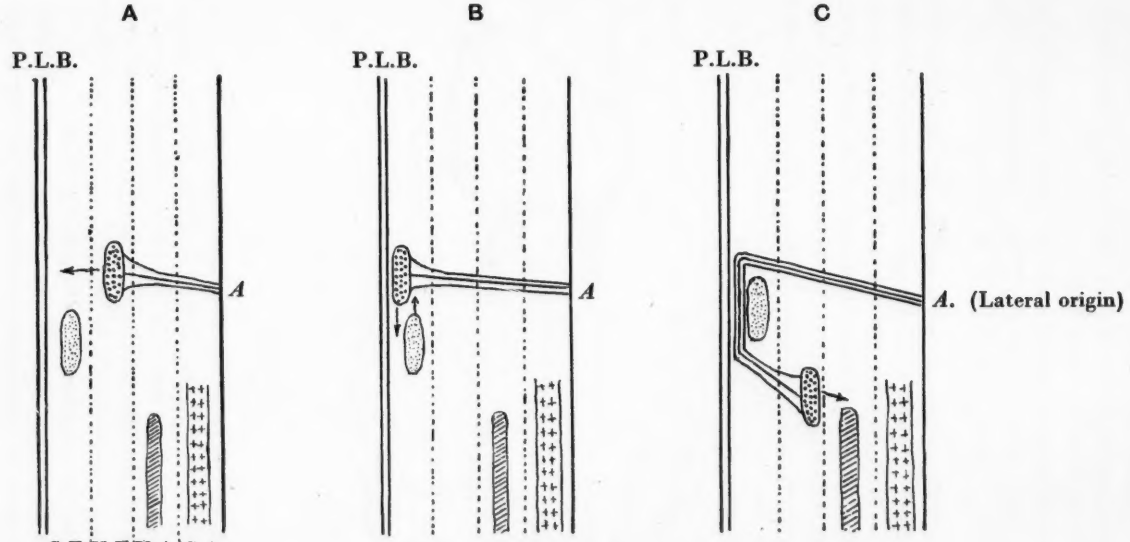
In many text-books of anatomy the possibility of the facial nerve receiving fibres from the oculomotor nucleus, *via* the posterior longitudinal bundle of the same side, is mentioned. According to Mendel's original work (3) on this subject, these fibres are destined for the supply of the upper facial muscles.

In four of the present series of dissections, a bundle of fibres, sufficiently strong to allow of dissection, was met with, descending from the homolateral posterior longitudinal bundle in its highest pontine part, to join the third part of the emergent facial root just beyond the genu. These fibres were not traced to their origin, but their presence affords some evidence for the above supposition. It is intended to investigate this matter more fully.

EXPLANATION OF THE INTRAPONTINE COURSE OF THE ROOT OF THE FACIAL NERVE

The motor nucleus of the facial nerve is classified by Herrick (2) and others as a visceral motor nucleus. It therefore arises lateral to the somatic motor column in which the abducens nucleus is developed. Again, Streeter (5) states that in the early human embryo the facial nucleus lies cephalic to the abducens nucleus. These two statements fix the original position of the facial nucleus as cephalo-lateral to the abducens nucleus (fig. 7 A).

The common explanation, based on the theory of neurobiotaxis (1), of the adult position of the facial nucleus is that, since it receives the bulk of its afferent stimuli from the nucleus of the spinal tract of the trigeminal nerve, it migrates, during its development, towards this source of stimulation, leaving its efferent fibres to mark the path it has followed in its migration. But, in order to leave its emergent fibres along the medial side of the VIth nucleus (as the second part of the root), the facial nucleus must first move medially. Possibly the fibres coming from the posterior longitudinal bundle, which have been seen in these dissections, provide the stimulus which causes this initial medial migration (fig. 7 B).



S.E. = somatic efferent
V.E. = visceral efferent
V.A. = visceral afferent
S.A. = somatic afferent

Motor nucleus of VIIth : coarse stippling
Motor nucleus of VIth : fine stippling
Nucleus of solitary tract : lined
Sensory nucleus of Vth : crossed

Fig. 7.

Then, having reached a position close to the mid-line, the VIIth nucleus moved caudally to the caudal end of the VIth nucleus, and eventually sank ventrally and laterally into its adult position close to the spinal nucleus of the trigeminal and the superior olive (fig. 7 C).

Thus a nucleus, starting from a position just beyond the genu of the adult facial root and travelling along the path described above, would leave its emergent fibres with a course corresponding to the first and second parts of the facial root.

The acute angle of the genu may be explained by the slight cephalic movement of the abducens nucleus which is said to occur (Streeter and Elliot Smith (5, 4)) towards its principal source of stimulation—the tegmental nuclei.

The third part of the facial root is the oldest part of the central course of the VIIth nerve and represents the path of the emergent fibres, arising from the VIIth nucleus in its original position, and passing to a lateral origin from the brain stem, as in fishes and amphibians (figs. 7 A and 8 A).

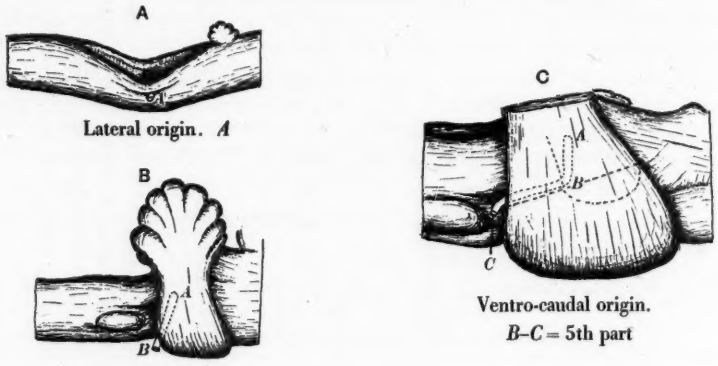


Fig. 8.

As the cerebellum and its peduncles developed, this lateral origin became bounded, cephalically by the superior peduncle, and caudally by the inferior peduncle, while the middle peduncle came to overlie the lateral exit of the nerve, thus ventroflexing it at this point and applying it to the lateral surface of the brain stem. Thus in mammals the nerve has a ventral point of emergence from the brain and the root has now a fourth part (fig. 8 B).

In the human brain, the cerebro-cerebellar connections are multiplied and in consequence the pons has undergone a considerable increase in size. The facial nerve, which in mammals made its exit at the caudal border of the pons, has now been pushed still further caudally by the rapid expansion of the pons, until in the adult human brain its superficial origin is ventro-caudal to

its earlier mammalian position, which is now represented by the flexure between the fourth and fifth parts of the root (fig. 8 C).

Thus the several parts of the adult intrapontine root of the facial nerve have positions and relations which have been determined by developmental changes, either in the position of the nucleus of origin, or in the architecture of the pons as a whole.

SUMMARY

1. The intrapontine course of the motor root of the facial nerve shows an anatomical division into five parts.

2. These five parts are marked off by well-defined flexures which occur at points where the presence of other structures necessitates a change in direction.

3. It is suggested that the course of the first two parts only is to be explained by neurobiotactic migration of the facial nucleus.

4. It is suggested also, that the explanation for the course of the remaining three parts is to be sought in the developmental history of the pons itself.

My sincerest thanks are due to Prof. J. S. B. Stopford for the kind interest he has shown in this work.

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THE STRUCTURE OF THE THORACIC INFERIOR VENA CAVA IN THE RABBIT AND IN THE CAT, AND ITS FUNCTIONAL SIGNIFICANCE

By K. J. FRANKLIN, D.M.

From the University Department of Pharmacology, Oxford

In connection with research on the venous return to the heart, I was forced to think that there must be a maximum point of distension for the inferior vena cava. This view I proceeded to test on a decapitate cat under artificial respiration. When the abdomen was opened the vena cava, just below the renals, had a diameter of 5·5 mm. I clamped it just above these veins, and tied in a glass cannula above the entry of the iliacs, after ligaturing all the tributaries in between. I then removed the contained blood, connected the cannula to a burette of Ringer-Locke solution at body temperature, and measured the diameter of the vena cava when exposed to a pressure of 65 cm. of the solution. It was still 5·5 mm. I stripped off the mesentery, and it was again 5·5 mm. There was, therefore, a point of maximum distension for the vein, as I had thought.

It seemed to me possible that the mechanism preventing further distension might be a criss-cross double spiral network of collagen fibres, and I have since examined various veins for such a structure. The results encourage me to continue the research, but the findings in the case of the thoracic inferior vena cava of the rabbit and of the cat form a definite entity, and I present them, therefore, separately as a preliminary communication.

One can remove part of the right thoracic wall of rabbits under ether, or of cats under chloroform and ether, and respiration and circulation will continue for some time, although one lung is collapsed. I have thus watched a rabbit for as long as twenty minutes, and the heart was quite well filled for each systole. In another rabbit the arterial blood pressure was over 110 mm. Hg at the end of ten minutes. Poiseuille (1), as long ago as 1830, showed that the venous return in dogs does not suffer overmuch by removal of the pressure variations within the thorax. It is fair to assume, then, that under these circumstances one is obtaining an approximately normal view of the movements of the diaphragm and of the vena cava. Except on strong contraction of the diaphragm, the position of the right auricle does not vary appreciably on inspiration. If the inspiration is very strong, the heart and vessels descend a little and the trachea lengthens. In either case, inspiration causes a decided lengthening of the thoracic inferior vena cava. Mettenleiter (2) found similar lengthening and lack of descent of the right auricle in dogs.

I measured the length of the inferior vena cava in the expiratory and inspiratory positions in rabbits and in cats, by the help of certain points on these veins. Then, in each case, I made a cut in the auricle, and through it inserted into the vein a long flanged glass tube of approximately the same calibre as the vessel. This was tied in at my upper point. Into the lower end of the vein I inserted a short flanged glass tube and tied it in at my lower point. The vein was then cut across outside the ligatures, and the tube-vein-tube system was washed clear of blood. The lower tube was closed, while the system was nearly full of water, and the upper tube was then clamped on a stand, so that the whole hung vertically with the vein distended by the pressure of fluid above.

It was found that at a certain length between the ligatures, corresponding to the expiratory length in the animal, the vein had a maximal volume, both shortening and lengthening causing a decrease. Stretching as far as possible caused a decrease from the maximum of 11/14 in the cat, and of 28/43 in the rabbit, and the calibre of the vein diminished from both ends towards the centre of its length. Rebound on release was very rapid and suggested the presence of elastic tissue; the rebound took the vein back to a length shorter than that at which it had its maximum volume.

I next brought a light and a magnifying glass into appropriate positions and dissected off an adventitia composed of longitudinal elastic fibres. (I have found since that this is more easily done if the vein is filled with air and the compressing fluid is above the vein.) Under the elastic fibres I discovered a double spiral network of fibres (fig. 1) which I suspected to be collagen. They show up slightly more clearly in the rabbit than in the cat, but can be seen in both with the naked eye; either spiral set can be emphasised at will by a slight twist of the lower glass rod. Repetition of the shortening and stretching showed that the volume variation was dependent on these fibres, and not on the elastic ones, and the maximum volume seemed to occur when the angle made by one set of spirals to the other was somewhat over 90°. Mr I. O. Griffith has kindly worked out a graph (fig. 2) for me, which confirms this; it is assumed that the fibres do not vary in length. The volume is theoretically at its maximum when the upper angle made by the tangent of each spiral to the long axis of the vein is about 55°, i.e., when the total angle is 110°. With the adventitia stripped off, there was still some rebound after stretching, which I thought was probably due to some smaller amount of elastic fibres in the intima.

It remained to test the volume variation *in situ*. This I did for both rabbit and cat as follows. I killed the animal by a blow on the head, opened the abdomen, ligatured the vena cava and the portal vein, and sewed up the wound. Then I opened the thorax, introduced a right-angled glass tube through the auricle and tied it in position in the upper end of the vena cava. The tube was then fastened with its open end upright in a rigid clamp. Care was taken to see that the upper end of the vein was at its previous distance from the

diaphragm. The vein and part of the vertical arm of the tube were filled with Ringer-Locke solution at body temperature, and the thoracic cavity warmed up with similar fluid. Stimulation of the right phrenic nerve or of the diaphragm caused a rise in the level of the fluid in the tube. The vena cava was now ligatured just above the diaphragm and the experiment repeated, with similar results.

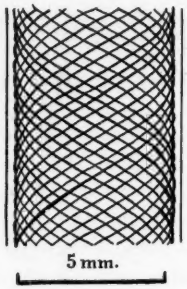

Fig. 1. The arrangement of the collagen fibres in the thoracic inferior vena cava of the rabbit, as seen through a magnifying glass, after dissecting away the elastic tunica adventitia. The vertical lines indicate the thickness of the elastic layer that is removed.

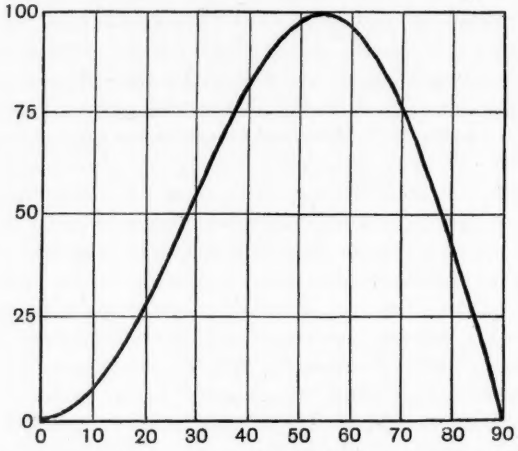

Fig. 2. Graph showing the relation between the angle, formed by the tangent to a spiral and the long axis of the vein, and the volume of the vein. It is assumed that the collagen fibres do not vary in length.

The histology of the veins was studied in two ways. I dissected out the spiral structure, as above described, in the two animals, and had the veins fixed in corrosive sublimate formol under pressure. They were then slit open, and stained with picro-indigo-carmine and orcein. The criss-cross structure

was visible, and proved to be collagen, but a good microphotograph was not obtainable owing to the thickness of the piece of vein, and the presence of sporadic elastic fibres of the adventitia. The total thickness of a distended vein wall is that of a sheet of paper, and it is therefore difficult to remove the adventitia properly. So I also had made longitudinal and transverse sections of the whole vein from both cat and rabbit. These were stained with picro-indigo-carmine and orcein, and with iron-haematoxylin and van Gieson. In both animals there are longitudinally directed elastic fibres in the intima. Outside these is a layer of collagen fibres, comparatively thicker in the cat and also, in the cat, containing a few fine elastic fibres. External to the collagen fibres is an adventitia of numerous longitudinally directed elastic fibres. There were no smooth muscle fibres in any of the sections.

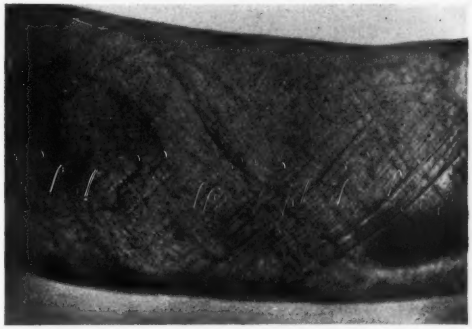

Fig. 3. Photograph showing the criss-cross of collagen fibres in a rabbit's thoracic inferior vena cava. × 7.

CONCLUSION

The thoracic inferior vena cava in the rabbit and in the cat consists of an adventitia and an intima containing longitudinally directed elastic fibres, which are especially numerous in the outer coat, and are capable of shortening the vein to a length smaller than that which it occupies in the expiratory position of the diaphragm. The media consists essentially of a criss-cross double spiral network of collagen fibres, which has a maximum volume at the length it assumes in the expiratory position of the diaphragm. The contraction of the diaphragm on inspiration therefore decreases the volume of the vein, provided the vein was fully distended before.

I wish to thank Mr Marsland, of the University Department of Physiology, Oxford, for the preparation of the histological specimens.

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THE CONSTITUTION OF THE LIGAMENTUM CRUCIATUM CRURIS

By T. T. STAMM, M.B., B.S.

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The fact that the tendons of the extensor digitorum longus are enclosed in a fibrous loop as they lie in relation to the ligamentum cruciatum cruris is well known. The attachments of this loop have been fully described by Retzius (1) in 1841 and again by Barclay-Smith (2) in 1896, and an accurate description of the connections of the ligament as a whole is given by Frazer in his *Anatomy of the Human Skeleton*. The loop referred to above is attached, laterally, to the anterior part of the upper surface of the calcaneus, and from its deep surface, near the medial end, a strong flattened band passes upwards and medially behind the tendons of the extensor hallucis longus and the tibialis anterior to reach the tibia. A second band passes from the extremity of the loop on a more anterior plane and runs in front of the extensor hallucis longus tendon. It is connected to the deep layer on the medial side of the tendon, and it may or may not be continued onwards to reach the tibia in front of the tibialis anterior tendon (fig. 1). From the deep aspect of the loop a second band passes downwards and medially and splits into two portions which are attached to the calcaneus and to the under surface of the neck of the talus respectively. These two parts at their attachment lie between the two constituent layers of the talo-calcaneal interosseous ligament. It was the curious connection to the neck of the talus that led me to examine the condition in other primates.

In the *Macacus Rhesus* the ligamentum cruciatum is represented by the ligamentum fundiforme, which forms a sling for the tendon of extensor digitorum longus and is only anchored at its lateral end, where it is attached to the anterior part of the upper surface of the calcaneus, as figured by Bland Sutton in his *Essays on Ligaments*. As he observed, in this animal the lower fibres of the ligamentum transversum hook laterally and downwards deep to the tendons of tibialis anterior and extensor hallucis longus to reach the calcaneus just deep to the ligamentum fundiforme, forming a sling for these tendons (fig. 2). Sir Arthur Keith (3) pointed out that this band persists in Man, as a constituent part of the ligamentum cruciatum cruris, and showed how it had become modified by the addition of new fibres from the deep fascia on a more anterior plane in order to meet the needs of the upright posture.

In the *Cercopithecus Sabaeus* a similar arrangement is present, but the fibres which curve round the tibialis anterior and extensor hallucis are now attached to the talus as well as to the calcaneus. They are quite distinct from

and have no connection with the ligamentum fundiforme (fig. 3). Through the kindness of Dr Zuckerman, the prosector to the Zoological Society of London, I was enabled to dissect this region in the leg of a chimpanzee. The general disposition of the ligaments was found to be similar to that in the *Cercopithecus*, but the oblique band had now become partially fused to the deep surface of the ligamentum fundiforme.

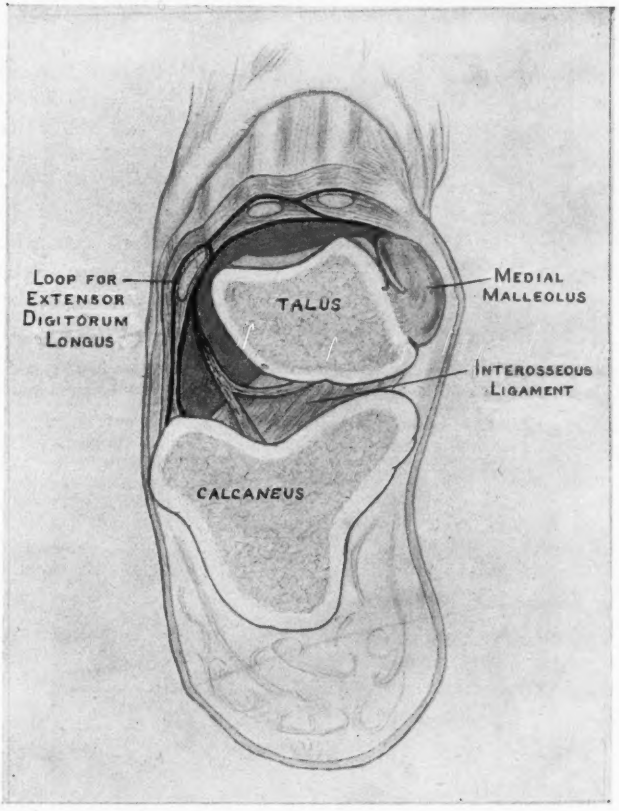

Fig. 1. Oblique coronal section through posterior part of right foot, to show the arrangement of the ligamentum cruciatum cruris.

It is clear that the curious attachment to the talus of the loop for the extensor digitorum longus tendons in Man is identical with the connection to the talus of the oblique band of fibres which passes behind the tibialis anterior and extensor longus hallucis in the lower forms. This attachment to the talus and to the calcaneus, as already noted, lies between the two layers of the talo-

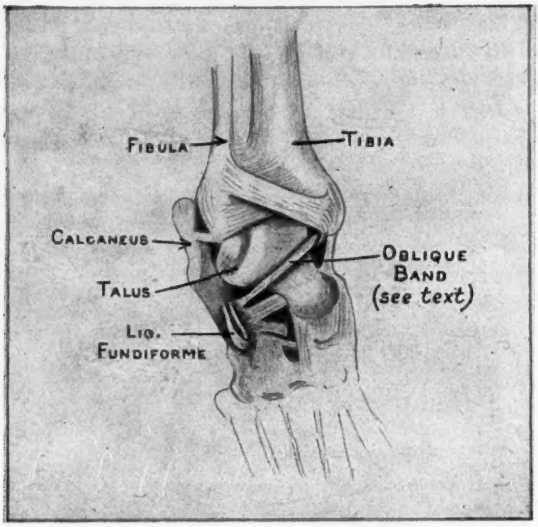

Fig. 2. Dissection of a *Macacus Rhesus* to show the ligamentum fundiforme, which has been turned forwards, and the disposition of the ligamentum transversum cruris.

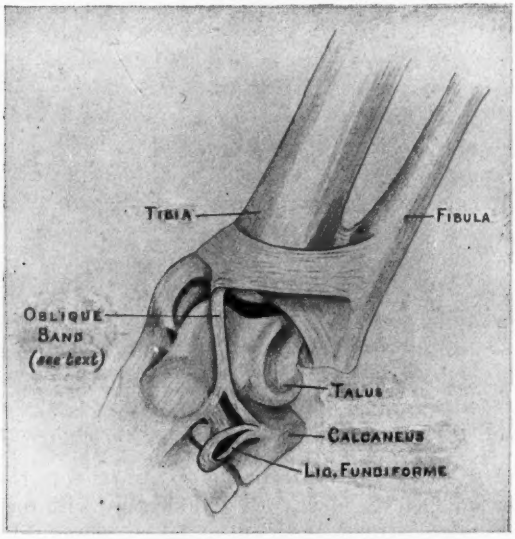

Fig. 3. Dissection of a *Cercopithecus Sabaeus* to show the modification in the disposition of the ligamentum transversum cruris.

calcaneal interosseous ligament. This ligament may therefore be considered as consisting of two lamellae which are the anterior and posterior ligaments of the articulations between the calcaneus and the body and head of the talus, respectively.

In the lower forms the frequent use of the foot in the inverted position necessitates the provision of loops to prevent the tendons from moving over to the medial side, a displacement which would interfere seriously with their efficiency. In Man, on the other hand, dorsiflexion is a much commoner and more important movement than inversion, and, in order that the efficiency of the muscles concerned may be maintained, it is necessary that the tendons should be held down on to the dorsum of the foot. This is effected by the development of new fibres on a plane anterior to the tendon of extensor hallucis longus. It is worthy of note that the tendon of tibialis anterior is only sometimes provided with an anterior retaining band, and this may be due to its more proximal insertion. But the relationship existing between the transverse crural ligament and the oblique band which passes behind the tendon persists, and still serves to prevent it from being displaced medially during the combined movements of inversion and dorsiflexion.

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THE SECONDARY OS CALCIS

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Pfitzner (1892) was the first writer to give a comprehensive account of the secondary os calcis. He described a series of 16 cases in which it was present. The accessory ossicle, although varying greatly in different subjects, presented in all cases certain characteristic features which allowed of definite identification, and established the bone as an anatomical entity.

Dwight (1907) describes two forms of secondary os calcis, one corresponding to the definite ossicle of Pfitzner, and the other non-typical type consisting of a projection from the front of the os calcis.

Bizarro (1920) mentions a case where a small secondary os calcis was associated with a vestige of a supratrochlear process of the astragalus and with accessory sesamoids. This writer points out the possibility of confusing a secondary os calcis with a secondary cuboid, although he admits the latter to be a doubtful anatomical entity. Both Dwight and Pfitzner definitely recognise the existence of the secondary cuboid, but, while the latter strenuously denies the possibility of the two accessory elements being identical, Dwight considers that it is not unlikely.

Krida (1923) has removed at operation a secondary os calcis which was apparently responsible for a disability still persisting 18 months after a sprain of the ankle.

Thurstan Holland (1928) describes how the bone can be shown radiographically.

The present paper deals with four specimens of the secondary os calcis which have been obtained from the Dissecting Room of the Department of Anatomy at the Otago Medical School during the last thirty years or so.

As to the frequency of the condition, Pfitzner found it in 16 cases out of 840 dissections, i.e. in 2 per cent. The Otago series give no reliable estimate of frequency, as it is likely that several cases have not been reported.

The literature contains little in the way of detailed description of the ossicle. To Pfitzner and Dwight we are indebted for such descriptions as are available. It has, therefore, been thought advisable in the present article to describe each specimen in some detail.

I have to acknowledge a debt of gratitude to Dr Gowland and Dr Durward for many helpful suggestions in connection with this paper.

DESCRIPTION OF THE SPECIMENS

Of the four specimens A, B, C, and D, the two first are from different subjects, while C and D are from the same body.

All the bones are in the interval between the os calcis and the head of the astragalus behind, and the cuboid and the scaphoid in front.

Specimen A

This is from the left foot of a subject of whom the age and cause of death are unknown. It is the largest bone of the series, and, judging from the available literature, the largest secondary os calcis yet recorded. The bone takes the

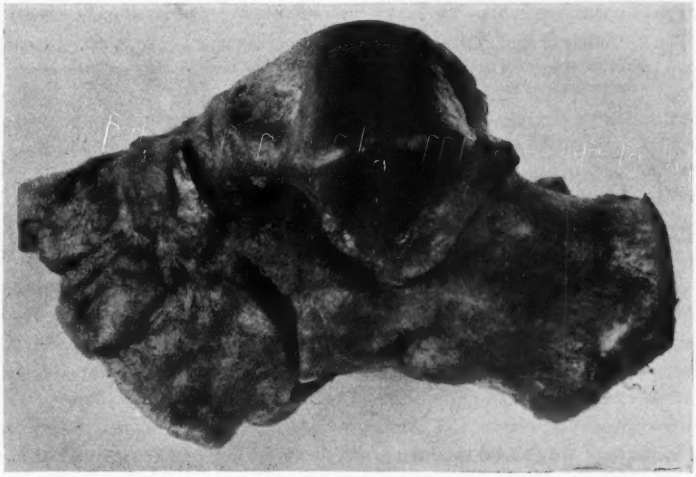

Fig. 1. Specimen A. Left foot. Showing the dorsal aspect of the accessory ossicle partially covered by the accessory process of the os calcis.

form of an irregular four-sided pyramid, 20 mm. in height, and of base 15 mm., with its long axis vertical. The base projects slightly from the dorsum of the foot (fig. 4). The secondary os calcis is attached behind to the os calcis and has definite articular surfaces for the astragalus and the cuboid. It reaches to within 6 mm. of the sole of the foot. The bone is tightly bound down to the external aspect of the scaphoid. There is an associated projection from the dorso-medial aspect of the anterior surface of the os calcis (figs. 1 to 5). This overhangs the accessory ossicle and is directed towards the scaphoid for a distance of 11 mm. Such a process is described by Dwight as a second non-typical form of secondary os calcis. The peroneal tubercle of the os calcis in this foot is particularly well developed. There are no available data concerning the other foot of the subject.

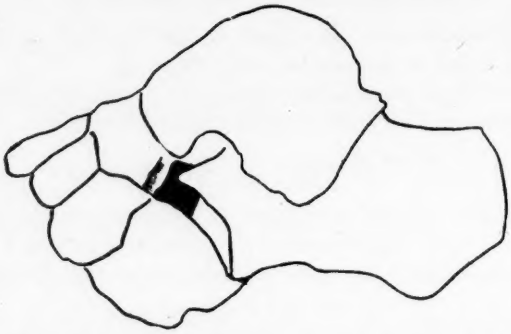

Fig. 2. Outline of fig. 1. The shaded line represents the attachment of the external calcaneo-scaphoid ligament (Chopart). In all the outline diagrams the black area represents the secondary os calcis.

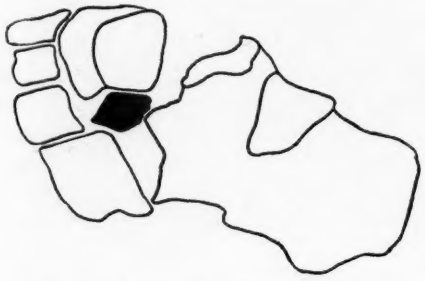

Fig. 3. Specimen A. Left foot. Outline from the dorsal aspect with the astragalus removed. The accessory process is seen directly posterior to the secondary os calcis.

Fig. 4. Specimen A. Left foot. Posterior aspect.

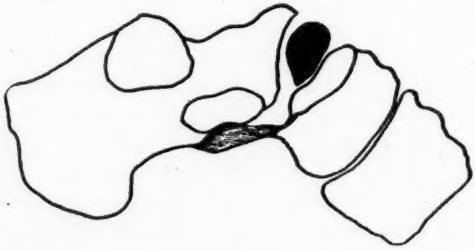

Fig. 5. Specimen A. Left foot. Outline from the internal aspect, showing the dorsal position of the accessory ossicle, and its distance from the spring ligament (shaded). The accessory calcanean process overhangs the secondary os calcis from the posterior aspect.

The ossicle may be described as presenting the following:

(1) Base.
(2) Apex.
(3) Postero-lateral surface.
(4) Postero-medial surface.
(5) Antero-lateral surface.
(6) Antero-medial surface.
(7) Anterior border.
(8) Posterior border.
(9) External border.
(10) Internal border.

(1) *Base*

This surface has an antero-posterior diameter of 15 mm. and its transverse measurement is 14 mm. It is situated dorsally and is seen on the dorsum of the foot, from which it projects for 2–3 mm. (figs. 1, 2 and 3). It is a diamond-shaped area in the interval between the os calcis, astragalus, cuboid, and scaphoid. The base is covered by the external calcaneo-scaphoid ligament (Chopart), which has no attachment to it.

(2) *Apex*

The apex of the pyramid lies between scaphoid and cuboid and reaches to within 6 mm. of the plantar aspects of these bones (fig. 5).

(3) *Postero-lateral surface*

A convex surface tapering towards the apex of the bone. It is bound by fibrous tissue to a concave area on the anterior aspect of the os calcis between the articular area for the cuboid and the sustentaculum. The upper part of this concave calcanean area is formed by a projection from the dorso-medial part of the calcanean facet for the cuboid, such as is described by Dwight as forming his second non-typical type of secondary os calcis. In this case the process is well developed and is directed towards the scaphoid. It projects 11 mm. in front of the anterior surface of the os calcis. The external calcaneo-scaphoid ligament (Chopart) stretches from this accessory calcanean process over the base of the ossicle to the outer dorsal edge of the scaphoid. It is a well-marked band (fig. 2).

(4) *Postero-medial surface*

This has a vertical extent of 19 mm., and an antero-posterior one of 10 mm. It is a plane, pyriform surface entirely covered with cartilage and articulating with the most lateral part of the articular area of the head of the astragalus. The presence of the accessory ossicle deepens the normal concavity with which the head of the astragalus articulates. This concavity is further accentuated by the presence of the spur from the anterior aspect of the os calcis.

(5) *Antero-lateral surface*

Dimensions: vertical extent 20 mm.; antero-posterior extent 10 mm.

This is a flat oval area, covered with cartilage except for the small part projecting from the dorsum. It articulates with the dorso-medial part of the posterior surface of the cuboid. The facet for the secondary ossicle is in the plane of the posterior surface of the cuboid, and is separated by a slight ridge

from the rest of the surface. This articulation is thus continuous with the calcaneo-cuboid joint.

(6) *Antero-medial surface*

A narrow, plane, roughened area, of maximum width 7 mm., tightly bound to the external aspect of the scaphoid, with which it is in contact. It extends almost to the plantar aspect of the scaphoid.

(7) *Anterior border*

This separates the antero-lateral surface, articulating with the cuboid, from the antero-medial surface which is bound to the scaphoid. It is a sharply defined margin lying in the interval between the scaphoid internally and the cuboid externally.

(8) *Posterior border*

This is sharply defined and lies along the anterior aspect of the os calcis in close connection with the accessory process of that bone mentioned above. It separates the os calcis from the articular margin of the head of the astragalus.

(9) *External border*

The external border is well defined and separates the calcanean postero-external surface of the secondary os calcis from the antero-external cuboidal area.

(10) *Internal border*

This lies along the external margin of the posterior surface of the scaphoid, to which it is attached.

SPECIMEN B

This is from a male subject who died of senility at the age of 75. The left foot shows the accessory ossicle, the right one being normal. Here the bone is a three-sided pyramid with its base plantarwards and long axis vertical. It measures 8 mm. across the base and has a height of 15 mm. This specimen does

Fig. 6. Specimen B. Left foot. The secondary os calcis is shown from the posterior aspect, indicating its close relationship to the plantar aspect of the foot.

Fig. 7. Specimen B. Left foot. The accessory ossicle has been removed to show the secondary cuboidal element at the plantar and external aspect of the scaphoid.

not reach the dorsum of the foot and the base is at the level of the plantar aspect of the scaphoid (figs. 6 and 8). It is in contact with the os calcis between the cuboidal facet of the latter and the sustentaculum tali, and has an articular surface for the cuboid. There is a roughened surface in contact with the head of the astragalus, but this is not covered with articular cartilage. The bone has

an anterior border which reaches to the lateral aspect of the scaphoid, to which it is attached. The scaphoid of this foot has a slight accessory backward projection from the plantar aspect of its posterior surface which is in contact with the lower 8 mm. of the anterior border of the secondary os calcis and has the appearance of being a secondary cuboidal element fused with the scaphoid (fig. 7).

Fig. 8. Specimen B. Left foot. From the internal aspect, showing the accessory os calcis as a plantar structure.

This secondary os calcis may be considered as having the following:

(1) Base.
(2) Apex.
(3) Posterior surface.
(4) Antero-lateral surface.
(5) Antero-medial surface.
(6) Anterior border.
(7) Postero-lateral border.
(8) Postero-medial border.

(1) *Base*

The base is irregularly triangular in shape and of width 8 mm. It is at the level of the plantar aspect of the scaphoid and is in contact with the spring ligament, to which it is not attached. Laterally the base is in relation with the short plantar ligament.

(2) *Apex*

This is directed dorsally, the long axis of the bone being vertical, in the interval between the cuboid and the scaphoid. The apex reaches to a distance of 13 mm. from the dorsum of the foot.

(3) *Posterior surface*

The largest surface, triangular in outline and roughened (fig. 6). It is convex and there is no definite border between it and the base of the bone. This surface is firmly attached to a roughened area on the os calcis between the cuboidal facet and the sustentaculum tali. This area extends on to the anterior part of the sustentaculum.

(4) *Antero-lateral surface*

This has a vertical measurement of 15 mm. and an antero-posterior one of 5 mm. It is oval in outline, slightly convex and cartilage-clad. This surface articulates with a narrow facet on the cuboid at the junction of its posterior and internal surfaces. The facet on the cuboid looks medially and slightly backwards and is almost at right angles to the posterior surface of the cuboid (fig. 6).

(5) *Antero-medial surface*

A small, roughened, slightly concave area in contact with the most external and plantar aspect of the head of the astragalus. This area on the secondary ossicle is not covered with articular cartilage.

(6) *Anterior border*

A sharply defined margin between the cuboidal and astragalar surfaces of the accessory bone. It lies between the cuboid and the scaphoid, being intimately related to the lateral articular border of the latter bone. This border of the secondary os calcis is firmly united along its whole length to the interosseous ligament between cuboid and scaphoid.

(7) *Postero-lateral border*

This separates the cuboidal from the non-articular calcanean area of the secondary bone.

(8) *Postero-medial border*

This separates the astragalar area anteriorly from the posterior calcanean area.

SPECIMEN C

This specimen is in the left foot of a man who died from a cerebral haemorrhage at the age of 70. The bone here is an almost vertical, oval plate, of height 20 mm., and of average thickness 5 mm. (fig. 10). The plate is thicker posteriorly. It is laterally compressed, its antero-posterior measurement being 9 mm., and the long axis is directed plantarwards and medially (fig. 9). The bone is attached to the os calcis and the scaphoid, and articulates with the cuboid and the astragalus over the whole of its lateral and medial surfaces respectively. This specimen extends from dorsal to plantar aspects of the foot. There is a secondary os calcis in the other foot of this subject.

Fig. 9. Specimen C. Left foot. Posterior aspect showing extent of ossicle from dorsum to sole of foot.

Fig. 10. Specimen C. Left foot. Outline from the internal aspect.

This ossicle may be described as having the following surfaces and borders:

(1) Posterior surface.
(2) Lateral surface.
(3) Medial surface.
(4) Anterior border.
(5) Superior or dorsal extremity.
(6) Inferior or plantar extremity.

(1) *Posterior surface*

This is a narrow area corresponding to the greatest thickness of the plate. It is roughened and in contact with a very roughened area on the anterior aspect of the os calcis between the cuboidal facet and the outermost portion of the sustentaculum.

(2) *Lateral surface*

An oval cartilage-clad area articulating with a definite facet 15 mm. in height and 8 mm. in width which is situated at the innermost part of the posterior articular surface of the cuboid. This facet on the cuboid for the secondary ossicle is directed backwards and slightly inwards and is separated by a definite ridge from the cuboidal articulation with the os calcis.

(3) *Medial surface*

A surface oval in outline and completely covered with articular cartilage. It articulates with the most infero-lateral part of the head of the astragalus. The area on the astragalus for the secondary ossicle is separated from the area for the scaphoid and that for the sustentaculum by definite ridges.

(4) *Anterior border*

This is bound down tightly along its whole length to the articular margin of the posterior surface of the scaphoid in its plantar and external aspects. This border corresponds to the long axis of the bone. It moves plantarwards and inwards. The anterior margin is also connected by fibrous strands to the interosseous ligament between cuboid and scaphoid.

(5) *Superior or dorsal extremity*

This corresponds to the upper narrowest part of the oval plate. It is slightly rounded and reaches the dorsal aspect of the foot in the interval between the os calcis and head of the astragalus behind and the cuboid and scaphoid in front.

(6) *Inferior or plantar extremity*

This is formed by the lowermost part of the plate and is on a level with the plantar aspects of the cuboid and the scaphoid. It is blunter than the superior extremity.

SPECIMEN D

This example of secondary os calcis is from the right foot of the subject from which specimen C was obtained. It is the smallest and least well developed of the series. There is present in the plantar aspect of the foot a small and irregular flat piece of bone invested in fibrous tissue which binds it to the os calcis and the scaphoid (fig. 11). It articulates with the astragalus and the cuboid.

The bone lies horizontally with its long axis almost transversely placed. From side to side it measures 14 mm. and antero-posteriorly 8 mm. This specimen is comparable to the secondary os calcis present in the foot of the other side. The plate of bone in the case of D is smaller and more a plantar structure. There are no other abnormalities in this foot.

Fig. 11. Specimen D. Right foot. The accessory ossicle as a small plantar structure.

This secondary os calcis may be described as having:

(1) Posterior surface.
(2) Supero-medial surface.
(3) Infero-lateral surface.
(4) Anterior border.

(1) *Posterior surface*

This is a narrow roughened area bound down to the os calcis in front of the facet for the head of the astragalus.

(2) *Supero-medial surface*

Dimensions: transverse, 12 mm.; antero-posterior, 8 mm.

This corresponds to the medial surface of C and articulates with the head of the astragalus. The change in direction of the astragalar surface here is due to the fact that the bone has become more completely a plantar structure than was its fellow of the opposite foot. It is doubtful if any articular cartilage is present on this surface of the accessory bone. It appears to be entirely bound up in fibrous tissue stretching from the plantar aspect of the os calcis to the scaphoid.

(3) *Infero-lateral surface*

This plane area is covered with cartilage and articulates with the more plantar part of the posterior surface of the cuboid. The facet on the cuboid is facing medially as well as posteriorly, and is almost at right angles to the remainder of the posterior surface of the cuboid.

(4) *Anterior border*

This is irregular and transversely convex. It lies along the plantar aspect of the posterior articular margin of the scaphoid, to which it is attached. The investing ligament of the secondary bone is not only attached to the border of the scaphoid but extends over the plantar surface of that bone in its external aspect.

CORRELATION OF ANATOMICAL DETAILS OF THE SPECIMENS

From the foregoing description it must be obvious that the accessory ossicle under consideration varies considerably in size and shape. It is, however, constant in its position relative to the other tarsal bones and remarkably constant in its articulations and attachments. The anatomical points will be discussed under the following headings:

(1) Size and shape.
(2) Position.
(3) Articulations.
(4) Attachments.
(5) Relationship to other abnormalities.

(1) Size and shape

The largest specimen, A, is a pyramid of height 20 mm. and base 13 mm. It has about the content of the os magnum of the carpus. The smallest, D, is an irregular plate of bone, 14 mm. by 7 mm., and has about one-third the content of A. The other two examples are intermediate in size. In that the largest bone is roughly three times the size of the smallest there is considerable variation in the size of the specimens under discussion.

Specimens A and B are definitely pyramidal in shape, the former of four sides and the latter of three. Specimen C is an oval plate and could be derived from B by laterally compressing the latter. Specimen D is irregular and more indefinite than the others. It is in the nature of a flat plate. The variation in shape of the bones is not so great as that in size. The first three correspond fairly well, but the fourth, being smaller and more irregular, is less readily compared.

(2) Position

All the accessory ossicles in this series are situated in the interval between the os calcis and the head of the astragalus behind, and the cuboid and the scaphoid in front. The only difference in position between members of the group is in their relation to the dorsal and plantar aspects of the foot. Two specimens (A and C) reach quite to the dorsum; the former having a definite surface at this aspect and even projecting beyond the dorsum. The apex of the pyramid which forms specimen B reaches only to within 13 mm. of the level of the dorsum.

In regard to their plantar relations, all the ossicles reach the sole of the foot except A, which is separated from it by an interval of 6 mm. It should be noted that the greater bulk of specimen A is towards the dorsum, whilst with B it is towards the sole. This is of importance in discussing the difference between the secondary os calcis and the secondary cuboid.

The base of B is lying on the short plantar ligament laterally and on the spring ligament medially, but is attached to neither of them. Specimens C and D are related to the same structures but not so intimately.

To summarise the matter of position we may say that specimen A is a

dorsal structure; B and D are plantar structures; whilst C is intermediate, extending from dorsum to sole.

(3) Articulations

All the accessory bones articulate with the cuboid, and the areas concerned are sharply defined and cartilage-covered.

Two of the series, A and C, definitely articulate with the head of the astragalus. The other two, particularly B, have surfaces in contact with that bone, but these areas are roughened and not covered by cartilage. There are no articulations with other tarsal bones.

(4) Attachments

All four specimens are related anteriorly to the interval between the cuboid and the scaphoid, and are in contact with the external aspect of the latter. They are also attached to the scaphoid and to the interosseous ligament between it and the cuboid. The area of contact with the scaphoid is particularly well marked in the case of specimen A.

All the bones described have areas in contact with the os calcis. These areas are constant in position, lying between the sustentaculum tali and the articular surface for the cuboid.

It would appear that the secondary os calcis is in all cases attached along the whole of its vertical extent to the scaphoid and to the tissue in the interval between this bone and the cuboid. There is a further constant attachment of the accessory ossicle to the os calcis, and attachments to other bones are absent.

(5) Relationship to other abnormalities

Pfitzner found that the most frequently associated abnormality was the tibiale externum, which occurred in four out of sixteen cases. In the present series there are no abnormalities which cannot be directly associated with the one under discussion, with the exception that specimen A has an exceptionally large peroneal tubercle.

Thus in specimen A there is a projection from the os calcis in relation to the ossicle. This is the projection which is described by Dwight as a second non-typical form of secondary os calcis. No other case has been recorded in which it has been found in conjunction with a definitely separate ossicle.

In specimen B there is a backward projection from the posterior surface of the scaphoid which gives the appearance of a secondary cuboidal element.

Pfitzner found bilateral secondary os calcis in two of his subjects. In the present series two of the cases, C and D, are from one subject; one case, B, had a normal opposite foot, and there were no data as to the opposite foot of the remaining specimen A.

DISCUSSION AND CONCLUSIONS

Four cases of a definite ossicle in one particular interval of the foot have been described. Two of these cases are associated with further accessory elements in the same interval.

Two questions arise for discussion:

(1) What distinguishes the secondary os calcis from the secondary cuboid, and can these structures be identical?

(2) What is the explanation of there being two accessory elements present in the same interval of the foot?

First we must define anatomically the two bones under discussion. The secondary os calcis is an accessory element appearing, in the majority of cases, near the dorsum of the foot between the os calcis, astragalus, cuboid, and scaphoid. It may be merged with the os calcis and appear as a process of that bone, or it may be a separate bone. It is attached to the os calcis and the scaphoid, and articulates with the cuboid and the astragalus.

The secondary cuboid is far less common. There are only two cases on record where it has been seen free. It, too, lies between the four above-mentioned bones, but it is usually fused either with the scaphoid or the cuboid. Dwight (1910) described a large free secondary cuboid which extended as far forward in the sole as the internal cuneiform. It measured 21 mm. anteroposteriorly and articulated with the os calcis, cuboid, and the head of the astragalus. This bone was attached to the scaphoid. I can find nothing in the literature as to what differences in shape may be expected between the two bones. Obviously they will both vary greatly in size.

It is thus seen that the only essential anatomical difference between the bones is one of dorsal and plantar relation. Pfitzner says emphatically that this fact suffices to differentiate between the two and establishes them as two entities. He adds that the secondary os calcis, as well as being dorsal, is more towards the fibula, and the secondary cuboid more tibial. Dwight, however, is not so definite and considers it possible that the two ossicles cannot be separated. In his opinion the secondary os calcis is not always a dorsal element, and he cites a case in point. I wish to stress this fact, because in the present series two of the bones, B and D, are definitely in the sole of the foot, yet I think they belong to the secondary os calcis type, for the following reasons: specimen B, although in the sole, does not project from it as does the secondary cuboid of Dwight; moreover the apex of the bone pushes well towards the dorsum. Furthermore this bone is definitely associated with a secondary cuboidal element fused with the scaphoid. In general, however, this specimen, B, much resembles a secondary cuboid.

Similarly, specimen D is a small and irregular bone in the plantar surface of the foot, but the other foot of this cadaver presents a definite secondary os calcis (specimen C). It is reasonable to assume that if one foot presents a secondary ossicle, any element in the same interval in the other foot will be of

the same derivation. This again shows that the secondary os calcis is not necessarily a dorsal element.

These two cases strengthen the view that the secondary os calcis and the secondary cuboid may be indistinguishable. The distinction between the two is much more difficult in those cases where the secondary os calcis has moved plantarwards.

For information in regard to the second problem concerning the presence of two accessory elements in the same interval we must turn to the work of Pfitzner, who advanced a plan of the hand and foot. The extremities were considered to consist of longitudinal rays made up of primary elements which were further arranged transversely. Each element was fated to do one of three things: it might disappear completely, progress isolated to the formation of an adult bone, or merge into an adjacent element.

Dwight has pointed out the usefulness of this theory in practice, but he adduces considerable evidence to show that it will not explain all bony anomalies of the extremities. He points out that one element may be present in the same member in two different places, citing the styloid element of the carpus as an outstanding example. A styloid element on the os magnum is frequently found associated with a knob on the adjacent metacarpal. Pfitzner has made no provision for this dual appearance of a single element. A possible and attractive explanation advanced by Dwight is that one of the added elements is an effort at repair on the part of a developmentally mutilated bone. Thus, when the styloid element fails to fuse with its metacarpal and does so with another bone, the metacarpal attempts to produce the normal from itself and the end result is the apparent appearance of the same accessory element in two places.

As has been mentioned, the secondary os calcis may appear as a separate bone or it may be a process of the adult os calcis. So far as I can find my specimen A is the only example of these two conditions occurring in the same foot. There is normally no projection from the anterior surface of the os calcis in the position described, therefore its presence in this case cannot be ascribed to any effort at repair on the part of a bone deprived of one of its elements. In this case the element producing the secondary os calcis is present in two places, first as a projection, and secondly as a separate ossicle.

The question arises—might not the separate ossicle be a secondary cuboid, which is said at times to be indistinguishable from the secondary os calcis? I think not, for the bone in question is a very dorsal structure and apart from this fulfils all the accepted conditions for a secondary os calcis.

Specimen B also shows the presence of two accessory elements in the interval between the os calcis, astragalus, cuboid, and scaphoid. It has been argued that the separate ossicle here is a secondary os calcis situated more plantarwards than is usual and the other accessory element is a secondary cuboid.

In conclusion it is maintained that specimen A definitely shows that a single primary element may appear in two places at once.

SUMMARY

(1) Four cases of secondary os calcis, two of which are from the same cadaver, are described in detail.

(2) It is argued that the secondary os calcis is not necessarily a dorsal structure in every case. When the secondary os calcis is placed towards the plantar aspect of the foot, it is practically indistinguishable from a secondary cuboid.

(3) It is shown that one of the specimens, A, has the secondary os calcis element present in two places at the same time. This cannot be explained by Pfitzner's theory as to the fate of the original elements of the extremities, nor can it be the effort of a developmentally mutilated bone to produce the normal.

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CIRCUM-AORTIC VENOUS RINGS

By P. N. B. ODGERS

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THESE two instances of a persistent circum-aortic venous ring were found in the bodies of elderly subjects in the dissecting room at Oxford during the past year.

Specimen I (fig. 1). Here a single left renal vein divided into ventral and dorsal branches directly after it had been joined by the left spermatic vein (*I.S.V.*). The ventral branch (*V.R.V.*) received the left suprarenal vein (*S.V.*) and ran normally in front of the aorta. The dorsal branch (*D.R.V.*) passed behind the aorta and, after being joined by the 2nd left lumbar vein and a left lumbar azygos vein, opened into the inferior vena cava just below the upper border of the 2nd lumbar vertebra (*2nd L.*) and about 1·5 cm. caudal to the ventral branch. There were no other abnormalities noted in the veins elsewhere in the abdomen.

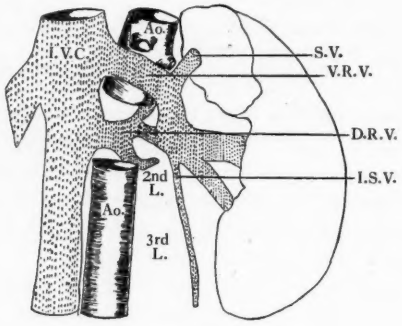

Fig. 1.

Specimen II (fig. 2). In this case there were two left renal veins, both the primitive renal veins presumably surviving. The lower and more ventral of the two bifurcated, its upper branch (*V.R.V.*) passing normally in front of the aorta and being joined by the left suprarenal and inferior phrenic veins (*S.V.*), while the lower branch after receiving the left spermatic vein (*I.S.V.*) was joined by the upper of the two renal veins. The trunk thus formed (*D.R.V.*) ran behind the aorta. It received here a communication from the 2nd left lumbar vein and the 3rd left lumbar vein and opened into the inferior vena cava just below the upper border of the 3rd lumbar vertebra (*3rd L.*). Except

that the left renal artery lay in front of the corresponding veins, there were no other abnormalities.

A search through the literature revealed only eight recorded cases of this persistent venous ring. Huntingdon and McClure, who described it as the Renal Collar in the embryo—"the formation of this subcardino-supracardinal anastomosis at about the level of the intersubcardinal anastomosis establishes the presence of a circum-aortic venous ring at this point, which we have designated the Renal Collar"—said they had seen it survive three times in the adult. The other five instances were published by Mutel and Fourche, who found it twice, by Nuzum, by Jeanbrau and Desmonts and by Walsham.

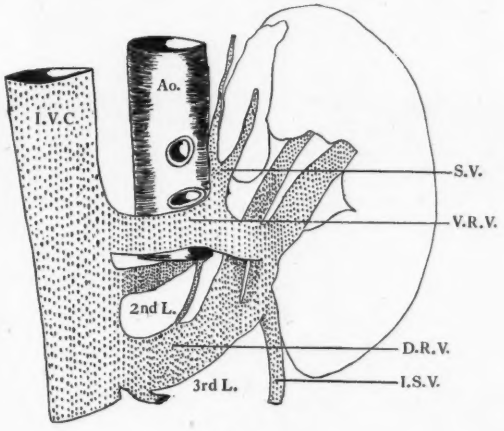

Fig. 2.

All the specimens described in detail are very similar to my first case. In one of these the left spermatic vein drained into the dorsal segment of the venous ring, as in my second figure, while in Walsham's case (of which I cannot find any reference beyond its mention by Mutel and Fourche) there was a reduplication of the inferior vena cava.

I do not suppose that this abnormality is as uncommon as one might gather from the very few instances of it which have been published, but it is, I think, less common than a persistence of the dorsal segment of the venous ring and the disappearance of its ventral half: in such cases a single renal vein will pass dorsal to the aorta.

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PAIRED OVIDUCTS IN THE FOWL

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In the developing chick paired Müllerian ducts are laid down symmetrically, one on either side of the body in male and female alike. As development proceeds, in the male both ducts degenerate, whereas in the female only the right duct atrophies, the left continuing its differentiation to become the functional oviduct.

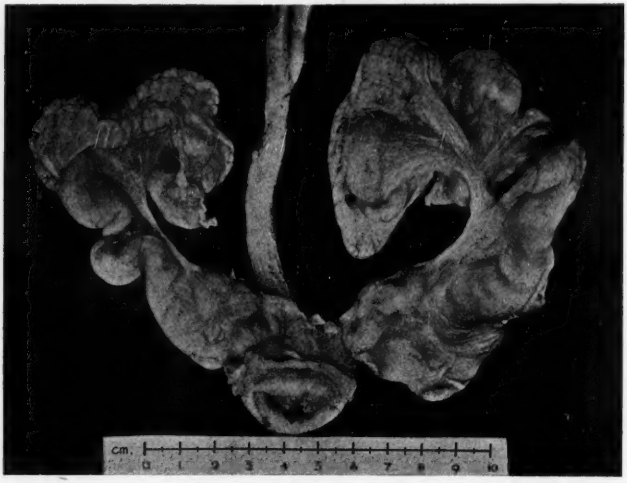

Fig. 1.

In the adult hen with a functional ovary and oviduct on the left and no discernible gonad on the right it is by no means uncommon, however, to find rudiments of a right oviduct. These rudiments range in size from a minute sac attached to the cloaca, to a blind, strongly convoluted tube, about 5 cm. long when extended, and 2 cm. wide, supported by a mesentery and distended by a clear watery fluid.

A right oviduct of greater size than this is a rarity. Shattock and Seligmann (1906), Parhon and Parhon (1922), and Crew (1923) have described cases of an unusually large right oviduct, but in each a testis was present on the right side of the body, and in none of them was the oviduct as large and as complete as that (fig. 1) of a Brown Leghorn which belonged to my colleague,

Dr A. W. Greenwood, to whom I am indebted for the specimen. This bird, hatched 27 May, 1929, and killed 18 July, 1930, carried a testis graft which had been implanted in infancy. She weighed 1600 grm. and a fully formed egg was found in the left oviduct. There was no perceptible gonad on the right, and the sinistral ovary was entirely normal in appearance and structure. The testis graft had persisted.

In view of the fact that Greenwood and Blyth (1930) have shown that one effect of a testis graft in a female is to retard and impair the development

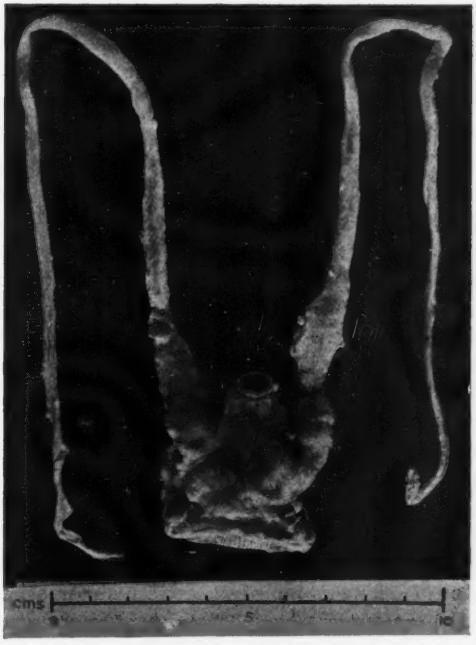

Fig. 2.

of the oviduct, it cannot be maintained that in this case, which was quite exceptional, the graft was in any way responsible for the development and very complete differentiation of the right oviduct.

Whilst this case was inviting explanation, another presented itself. A Wyandotte hen, hatched 1929, was sent to the Department from a Laying Trial for examination and report. It had never been known to lay an egg, yet it had every appearance of being about to do so. She was killed 7 October, 1930. The plumage was typically henny and her head furnishings were as those of a normal hen of her breed. She weighed 2600 grm. Her left ovary was degenerate. There was no discernible gonad on the right side. On either side there was a non-convoluted oviduct (fig. 2).

Disregarding the testis graft, it is seen that in Case I a normal left ovary is associated with completely differentiated left and right oviducts, whereas in Case II a degenerate left ovary is associated with left and right oviducts of a size and degree of differentiation equal to those of a non-laying hen. These facts support the generally accepted conclusion that the degree of structural complexity of the oviduct is imposed thereupon by the degree of physiological activity of the ovary. But this does not explain the presence of a right oviduct in these cases. Ordinarily, forces are exerted early in ontogeny which in the female chick lead to the more or less complete disappearance of the right Müllerian duct, and in the case of the male to the disappearance of both. The facts that rudiments of the right oviduct are commonly encountered in the normal hen and that these rudiments vary considerably in size permit one to assume that these forces which impose atrophy on the right oviduct vary, in different individuals, in strength, or, more probably, in time of exhibition. Thus, if the time during development at which these forces are exhibited varies from case to case, then the relative degree of development of the right oviduct can serve as a rough indication of the extent of delay in their exhibition: the larger the rudiment, the greater the delay. If this be so, then it is not surprising that exceptionally a case of a fully developed right oviduct should be encountered. Should a right oviduct be present, then it will react to the physiological stimulus of the left ovary, and its differentiation will be complete. It may be assumed, further, that if and when a right oviduct is thus allowed to develop unchecked, there comes a time when the degree of its development is such as to render it incapable of responding to the atrophy-provoking stimulus if and when this is subsequently exhibited.

Manifestly, there is a difference between right and left oviduct in the case of the normal hen. On the left side there are ovary and functional oviduct, on the right a rudimentary right oviduct. The degree of development of the right oviduct is not determined by the presence or absence of a right ovary, of a right testis, or of a hypertrophied imperfectly differentiated right gonad, as is shown by the cases now described and by the observations of Domm (1927). One must conclude that right and left Müllerian ducts differ one from the other in respect of their thresholds of response to the atrophy-provoking stimulus, whatever this may be, that of the right being lower than that of the left, so that this disappears, whilst the latter persists; and that in the male the stimulus overtops the thresholds of both right and left, so that both undergo atrophy.

Now that the sex hormones are coming to be available in relatively pure form, the validity of this attempted explanation can be put to the test of experimentation, for it is probable that the atrophy-provoking stimulus is hormonic.

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ON THE DEVELOPMENT OF THE HYOID BAR AND RAYS IN PLAGIOSTOMI

By F. H. EDGEWORTH, M.D.

A DETAILED account of the hyoid bar and rays of Plagiostomi was given by Gegenbaur in 1872. He stated that in Selachii the hyoid bar consists of upper and lower portions—the hyomandibula and the hyoideum[1], whilst in Batoidei the hyoideum extends upwards behind the hyomandibula and has varied dorsal attachments. Rays are attached to both the hyomandibula and the hyoideum in Selachii, but only to the hyoideum in Batoidei.

A new theory of the morphology of the hyoideum in Batoidei was advanced by Krivetski in 1917. According to him "l'arc hyoïde fondamental est représenté chez les requins par l'hyomandibulaire et par l'hyoïdeum; chez les raies il ne reste que le premier de ces deux éléments, l'hyoïdeum s'atrophie et est remplacé chez eux par le pseudohyoïdeum, c'est à dire un petit arc supplémentaire formé par la fusion des bouts proximaux des rayons."

The paper is written in Russian[2], with an abstract in French. The theory is based on the embryology of *Torpedo ocellata*, of which two figures are given—one of a horizontal section through an 18 mm. embryo, and the other of a model made from a 25 mm. embryo. In the latter an artery marked "com." is depicted arising from the gill-lamellae on the anterior wall of the 2nd gill-cleft, and passing forwards internal to the pseudohyoideum and external to the hyomandibula. No details are given in the text of the paper, either in the Russian one or in the French abstract. Thus the stages in which the hyoideum atrophies, and in which a pseudohyoideum is formed by fusion of the proximal ends of the rays, are not stated.

The information is thus very scanty, and is quite insufficient to prove the theory. No opinion of Gegenbaur can be so lightly dismissed.

de Beer (1926) gave descriptions of the skull of *Torpedo marmorata* in the 22 and 24 mm. stages, but did not investigate earlier ones. He accepted Krivetski's opinion, and stated that the position of the cross-commissure between the efferent branchial arteries lateral to the hyomandibular and to the branchial arches, but median to the posterior arch, confirmed it.

In view of this state of knowledge it appeared advisable to investigate the development of the hyoid bar and rays in various Selachii and Batoidei.

Embryos of *Torpedo ocellata* of 13, 15, 17, 17·5, 20, 20·5, 25 and 27 mm. were available.

In the 13 mm. embryo (fig. 1) the hyoid bar is not yet developed. In one of 15 mm. (fig. 2) it is formed as a continuous dorso-ventral structure, convex laterally and concave internally. Embryos of 17 and 17·5 mm. (fig. 3) show the same conditions. The bar has extended slightly upwards and downwards.

[1] The names used by Gegenbaur are "Oberes Stück" or "Hyomandibulare" and "Unteres Stück." I do not know who introduced the term "hyoideum" for the latter.

[2] Kindly translated for me by Dr Nierenstein.

In an embryo of 20·5 mm. (figs. 4 and 5) the bar is still a continuous dorso-ventral structure. Three rays are present. They project from and are continuous with the lower part of the bar. In the horizontal sections (figs. 6 and 7) of a slightly younger embryo the rays are partially but not fully continuous with the posterior surface of the bar. (This want of full continuity is shown better in fig. 8, which is at a higher magnification.) The rays are not outgrowths of the bar but independent formations which fuse with it. The most dorsal ray projects laterally and dorsally and the upper horizontal section (fig. 6) cuts across its lateral extremity. Owing to the position of the rays in relation to the bar they are not visible in the more anterior of the two transverse sections depicted (fig. 4). There is no trace of a pseudohyoideum posterior to the lower part of the bar in either embryo.

The condition of the arteries in the 20 and 20·5 mm. embryos is shown in figs. 4 to 7 and in the diagram in fig. 28. The 4th branchial efferent artery joins the median dorsal aorta and the anterior three the lateral dorsal aorta. They pass upwards anteriorly to their respective bars. The hyoid afferent artery passes to the outer border of the gill-lamellae on the anterior side of the 2nd gill-cleft. The emerging hyoid efferent artery passes to the back of the lower part of the hyoid bar and then upwards and inwards to the inner side of its upper part. It then passes forwards and joins its fellow just behind the pituitary body to form a median vessel which bifurcates into the two internal carotid arteries. The mandibular afferent artery is given off from the lower end of the hyoid efferent artery and passes forwards to the outer border of the gill-lamellae on the anterior side of the 1st gill-cleft. The emerging mandibular efferent artery joins the internal carotid artery.

The portion of the lateral dorsal aorta from the dorsal end of the 1st branchial efferent artery to that of the hyoid efferent artery disappears between the stages of 13 and 15 mm. (cf. figs. 1 and 2).

There is no vessel passing internal to the lower part and external to the upper part of the hyoid bar. This also holds for the 25 mm. stage when the hyoid bar has separated into dorsal and ventral portions.

In an embryo of 25 mm. (figs. 9, 10 and 11) the hyoid bar has separated into the hyomandibula and the hyoideum. The former is slightly chondrified. Its dorsal end articulates with the auditory capsule. Its ventral end is tied to the posterior end of Meckel's cartilage by a ligament. The hyoideum, still procartilaginous in structure, has extended upwards and backwards, and its dorsal end is posterior to the lower part of the hyomandibula. Four more rays have developed. All seven are continuous with the posterior surface of the hyoideum. There is no pseudohyoideum.

The conditions in a 27 mm. embryo are similar.

In a 15·5 mm. embryo of *Torpedo marmorata* the hyoid bar is beginning to develop, and in the same embryo the lateral dorsal aorta between the dorsal ends of the 1st branchial efferent and the hyoid efferent arteries is partially obliterated. This vessel is patent in a 10 mm. embryo. The sub-

sequent developmental stages of the hyoid bar and rays are as in *Torpedo ocellata*.

The development of the hyoid bar and rays in *Raja clavata* is similar to that in *Torpedo*. The bar is formed as a continuous dorso-ventral structure in a 30 mm. embryo. In an embryo of 48 mm. (figs. 12 and 13) it is still a continuous dorso-ventral structure. Five rays have developed postero-laterally to the lower part of the bar. Their inner ends are quite free from and posterior to the bar. This stage in the development of the hyoid bar and rays is slightly less advanced than that of the 20·5 mm. embryo of *Torpedo ocellata*. In an embryo of 52 mm. (figs. 14, 15 and 16) the hyoid bar has separated into the hyomandibula and the hyoideum. The latter has extended upwards and backwards behind the hyomandibula. Nine rays are present. Their inner ends are continuous with the posterior surface of the hyoideum. There is no pseudohyoideum in any of these embryos. The arteries are as in *Torpedo*. The portion of the lateral dorsal aorta between the dorsal ends of the 1st branchial and the hyoid efferent arteries is present in a 22 mm. and absent in a 30 mm. embryo.

These phenomena show that the bar depicted in the models of Krivetski and de Beer and named pseudohyoideum is, in reality, the hyoideum. The proximal ends of the rays, which are independent formations, become continuous with its posterior surface. There is no artery passing internal to the hyoideum and external to the hyomandibula.

In *Scyllium canicula* the hyoid bar is first visible in a 23 mm. embryo, as a continuous dorso-ventral structure. Figs. 17 to 19 are taken from a 28 mm. embryo, in which the bar is better marked. No rays are present. In a 30 mm. specimen (fig. 20) the hyoid bar is still a continuous structure. Three rays have developed postero-lateral to that portion of the bar which, from comparison with figs. 23 to 26, would have become the lower part of the hyomandibula. Horizontal sections (figs. 21 and 22) of another embryo of the same length, in which two rays are present, show that they are quite free from the bar. In an embryo of 35 mm. (figs. 23 to 26) the bar has separated into the hyomandibula and the hyoideum. Rays have developed in relation to both cartilages. In a 36 mm. embryo (fig. 27), in which chondrification is better marked, the upper rays are continuous, by dense non-chondrified tissue, with the postero-lateral surface of the hyomandibula and the dorsal part of the hyoideum. The most ventral rays are still free.

The development of the hyoid bar and rays in *Acanthias vulgaris* is similar to that in *Scyllium*.

The arteries of *Scyllium* and *Acanthias* are not quite identical with those of *Torpedo* and *Raja* (*vide* fig. 28). In the two Batoidei the three anterior branchial efferent arteries join the lateral dorsal aorta, in the Selachii only the 1st branchial does, i.e. the median dorsal aorta extends a little further forwards in the Selachii. In the Batoidei the portion of the lateral dorsal aorta between the dorsal ends of the 1st branchial and the hyoid efferent arteries disappears in early stages, at about the period when the hyoid bar begins to

develop. In the Selachii this portion also atrophies[1], but at a later stage, after chondrification and separation of the hyoid bar into dorsal and ventral portions. In other respects the arteries of this region are similar in the four genera.

The above evidence shows that the hyoid bar in the four genera of Plagiostomi investigated is developed as a continuous dorso-ventral structure. It separates into dorsal and ventral portions—the hyomandibula and the hyoideum. In the Selachii the hyoideum remains in its original position, in the Batoidei it extends upwards behind the hyomandibula. The hyoid rays are developed postero-laterally to an already formed bar, and their inner ends fuse with its postero-lateral or posterior surface. Some are developed before and others after the separation of the bar into dorsal and ventral portions. In the Selachii they are formed in relation to both the hyomandibula and the hyoideum, in the Batoidei solely to the latter.

It may be added that in all four genera the rays attached to the first four branchial bars are, similarly, of independent origin. Their inner ends fuse with the bars, some before and others after separation of the bars into discrete elements. No pseudobranchialia replacing any portions of the original bars are formed.

The embryos described above were obtained from Plymouth and Naples, and I am indebted to Dr Allen and Dr Dohrn for fixing and preserving them so well.

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LEGENDS TO FIGURES 1 TO 28

Fig. 1. *Torpedo ocellata.* Embryo 13 mm. Transverse section.

Fig. 2. *Torpedo ocellata.* Embryo 15 mm. Transverse section.

Fig. 3. *Torpedo ocellata.* Embryo 17 mm. Transverse section.

Figs. 4 and 5. *Torpedo ocellata.* Embryo 20·5 mm. Transverse sections. Fig. 5 is 0·11 mm. behind fig. 4.

Figs. 6 and 7. *Torpedo ocellata.* Embryo 20 mm. Horizontal sections. Fig. 7 is 0·09 mm. below fig. 6.

Fig. 8. *Torpedo ocellata.* Portion of fig. 7 at a higher magnification.

Figs. 9, 10 and 11. *Torpedo ocellata.* Embryo 25 mm. Transverse sections. Fig. 10 is 0·18 mm. behind fig. 9, and fig. 11 is 0·31 mm. behind fig. 10.

Figs. 12 and 13. *Raja clavata.* Embryo 48 mm. Horizontal sections. Fig. 13 is 0·29 mm. below fig. 12.

Figs. 14, 15 and 16. *Raja clavata.* Embryo 52 mm. Transverse sections. Fig. 15 is 0·12 mm. behind fig. 14, and fig. 16 is 0·075 mm. behind fig. 15.

Figs. 17, 18 and 19. *Scyllium canicula.* Embryo 28 mm. Transverse sections. Fig. 18 is 0·06 mm. behind fig. 17, and fig. 19 is 0·06 mm. behind fig. 18.

[1] In *Scyllium* the arteries atrophy at the 36 mm. stage. In *Acanthias* atrophy is beginning on one side at the 37 mm. stage, and is complete on both sides in the 48 mm. stage. It takes place by proliferation of cells into the lumen of the vessel.

Fig. 20. *Scyllium canicula.* Embryo 30 mm. Transverse section.

Figs. 21 and 22. *Scyllium canicula.* Embryo 30 mm. Horizontal sections. Fig. 22 is 0·1 mm. below fig. 21.

Figs. 23 to 26. *Scyllium canicula.* Embryo 35 mm. Fig. 24 is 0·16 mm. behind fig. 23, fig. 25 is 0·15 mm. behind fig. 24, and fig. 26 is 0·05 mm. behind fig. 25.

Fig. 27. *Scyllium canicula.* Embryo 36 mm. Horizontal section.

Fig. 28. Diagram of arteries in *Scyllium, Acanthias, Torpedo* and *Raja.* The portion of the lateral dorsal aorta which atrophies is represented by a line of dots.

ABBREVIATIONS OF NAMES USED IN THE FIGURES

Add. br.	Adductor arcus branchialis.
Add. mand.	Adductor mandibulae.
basihy.	basihyale.
br. bar	branchial bar.
br. eff. art.	branchial efferent artery.
br. ray	branchial ray.
Const. br.	Constrictor branchialis.
Const. br. superf.	Constrictor branchialis superficialis.
Const. dors.	Constrictor dorsalis (of the masticatory muscles).
Const. hy.	Constrictor hyoideus.
Depr. rostri	Depressor rostri.
dors. div.	dorsal diverticulum (of a gill-cleft).
dors. sp. ms.	dorsal spinal muscles.
electr. cols.	columns of the electric organ.
epibr.	epibranchiale.
Gass. g. V	Gasserian ganglion.
Genic. g. VII	Geniculate ganglion.
Genio-cor.	Genio-coracoideus.
hy. aff. art.	hyoid afferent artery.
hy. eff. art.	hyoid efferent artery.
hy. m. pl.	hyoid muscle plate.
hyomand.	hyomandibula.
hypobr. sp. ms.	hypobranchial spinal muscles.
int. car. art.	internal carotid artery.
Interbr.	Interbranchialis.
Interhy.	Interhyoideus.
Intermand.	Intermandibularis.
keratobr.	keratobranchiale.
lat. ceph. v.	lateral cephalic vein.
lat. dors. aorta	lateral dorsal aorta.
Lev. hyomand.	Levator hyomandibulae.
Lev. rostri	Levator rostri.
mand. aff. art.	mandibular afferent artery.
mand. eff. art.	mandibular efferent artery.
Meck. cart.	Meckel's cartilage.
otic. proc. palquad.	palatoquadrate.
phbr.	pharyngobranchiale.
posttrem.	posttrematic.
pretrem.	pretrematic.
R. hyomand. VII	R. hyomandibularis of the VII nerve.
Rect. cerv.	Rectus cervicis.
Roman figures	cranial nerves.
tr. ms.	trunk myotomes.
X.	vagus.
X_1	branch of the vagus to the 2nd branchial arch.

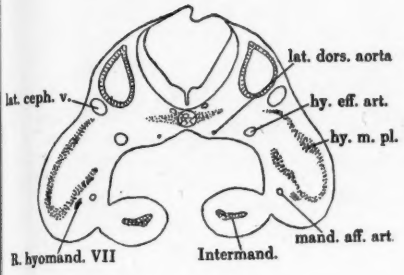
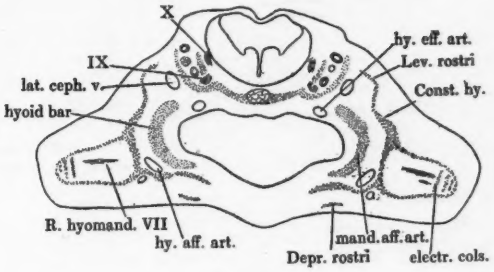


Fig. 1.



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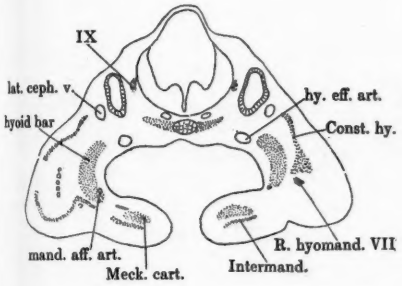

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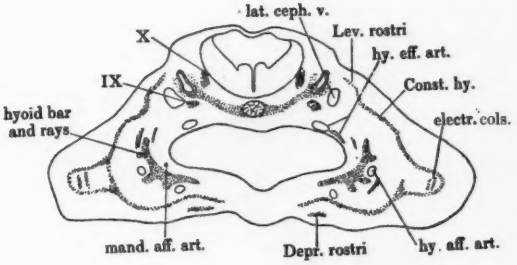

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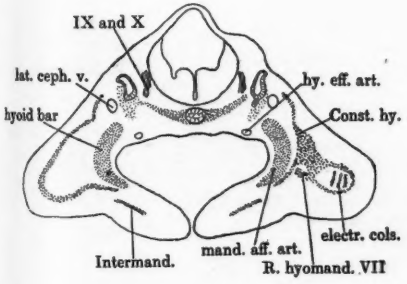

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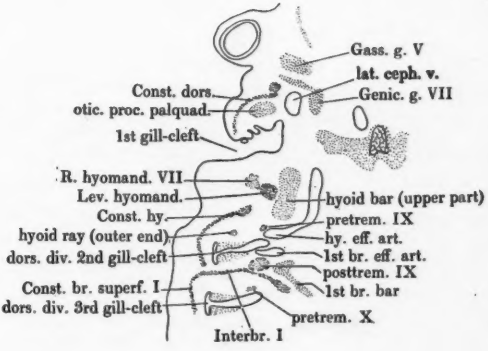

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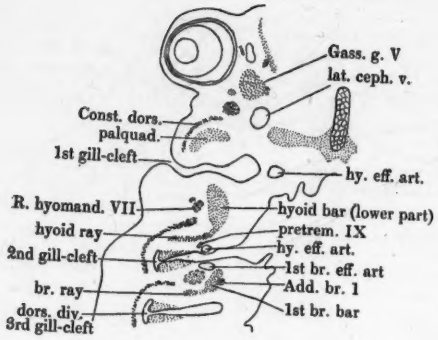

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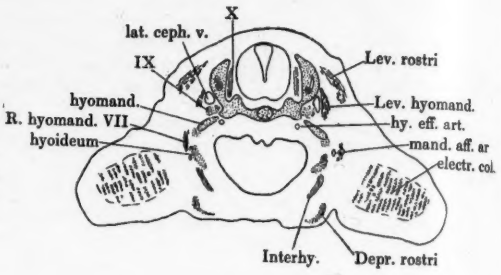

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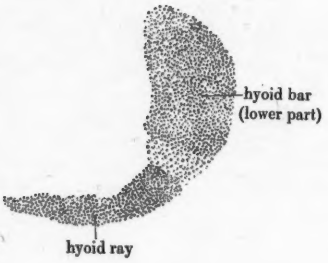

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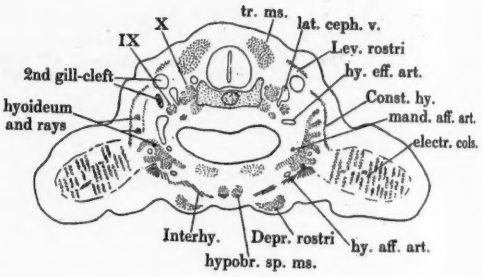

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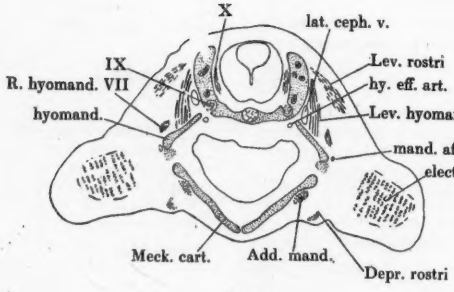

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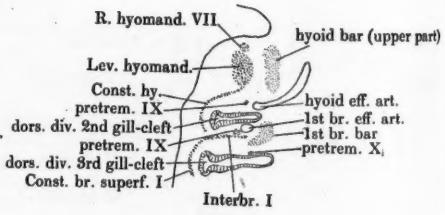

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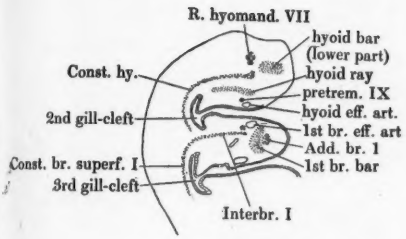

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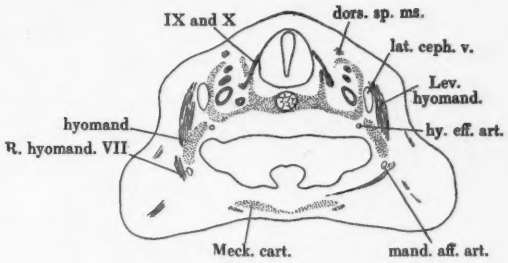

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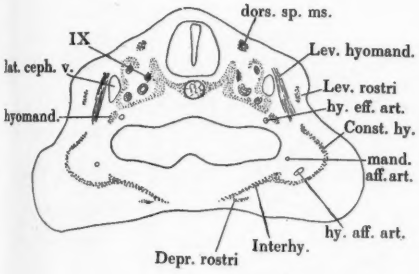

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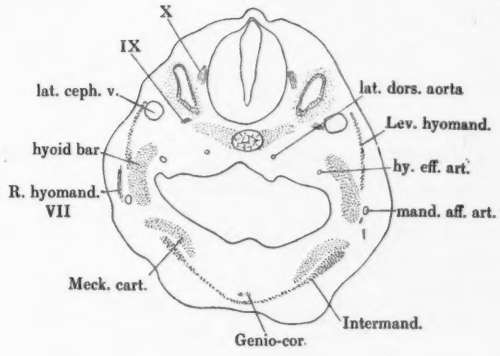

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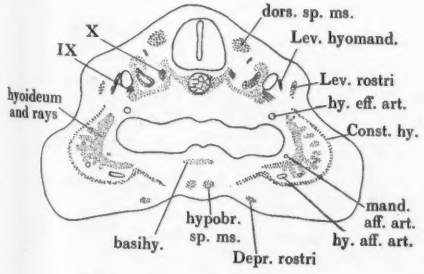

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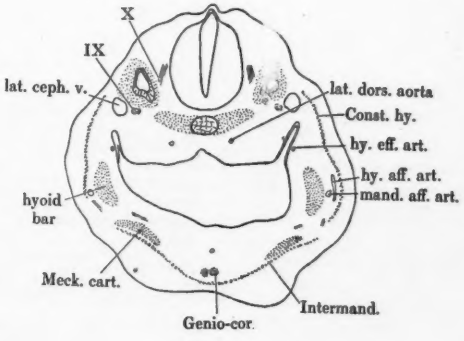

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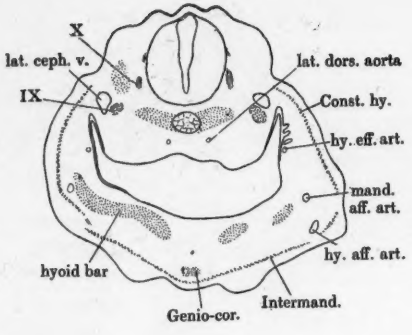

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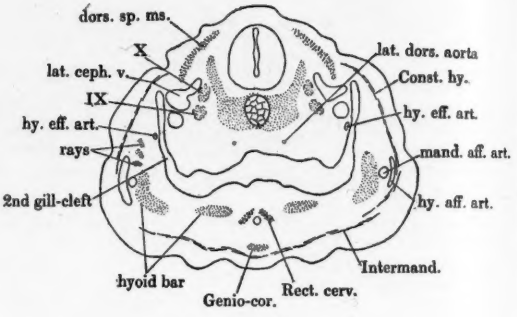

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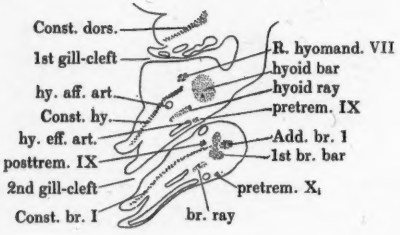

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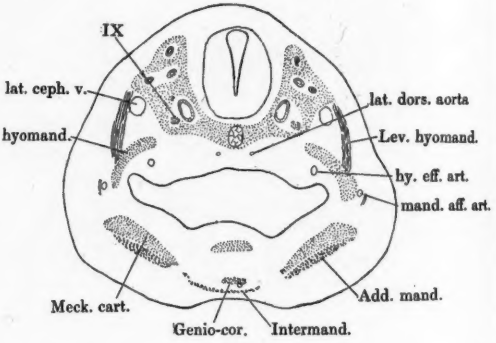

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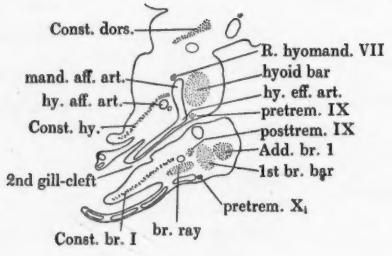

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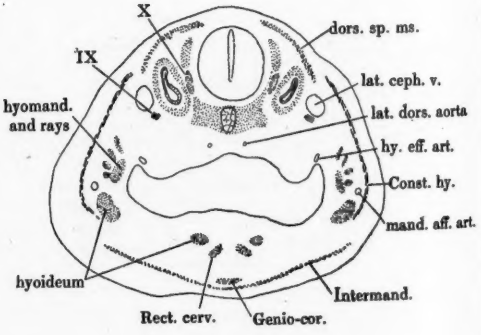

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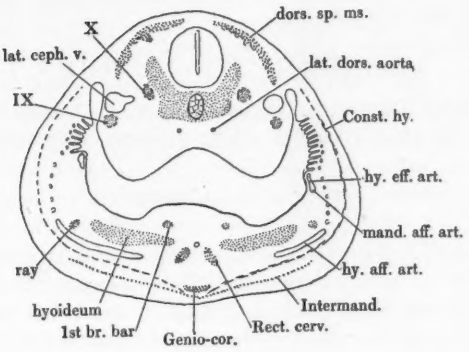

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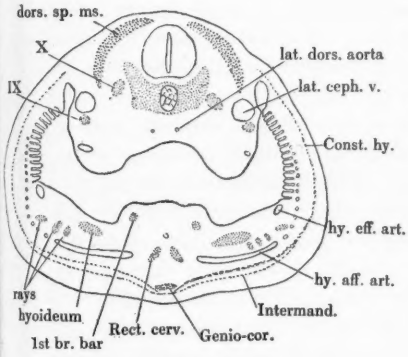

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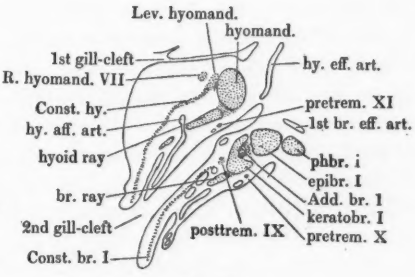

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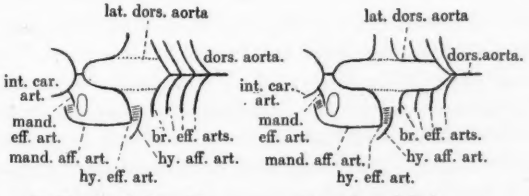

Scyllium and *Acanthias*. *Torpedo* and *Raja*.

Fig. 28.

CRANIOMETRIC MEMOIRS

No. IV. HORIZONTAL ZONES OF THE FACIAL NORMA IN MODERN AND FOSSIL MAN

By JOHN CAMERON

THE idea of mapping off the facial norma of the skull into horizontal zones first suggested itself to the author in 1919, while he was engaged in making a craniometric report on the alleged Micmac skull in the Nova Scotia Provincial Museum. The procedure adopted at that time is best described in the author's actual words (1): "Horizontal lines were drawn through the nasion, the lower borders of the orbits, the akanthion and the prosthion respectively. These divided the face (i.e. from the nasion to the prosthion) into upper, middle and lower horizontal areas. On studying the relative proportions of these, it was observed that the middle and lower areas were approximately equal in depth, while the uppermost was distinctly more extensive in its vertical dimensions than the other two. The points through which these lines are drawn are, with the exception of the lower orbital margins, recognised as fairly constant in position, though in the case of this Micmac skull the position of the prosthion could be only approximately determined, owing to slight deficiency of the alveoli of the incisor teeth. Still it was considered possible that this method of studying the norma frontalis of the skull might be utilised as an additional criterion for determining the race of any given skull. I have so far not applied this method to anything like an extensive series of crania, and am therefore unable at present to make any definite pronouncement as to its value or otherwise. However, I found that the three horizontal areas in a Melanesian skull exhibited a very decided degree of difference from those of this Micmac skull in regard to their relative proportions. Fig. 10 has been designed to demonstrate this comparative difference. The Micmac skull is not drawn to the same scale as the Melanesian skull. In the latter the lower horizontal area shows a marked reduction in depth, when compared with the Micmac skull, and is due of course to pronounced foreshortening, the result of an excessive degree of prognathism in this case. On examining the two upper horizontal areas in the Melanesian skull, it is at once observed that they are almost exactly equal in depth. It is evident, then, that this method disclosed a very profound interracial difference, so far as these two individual skulls were concerned. Indeed, the results look so hopeful and encouraging, that I intend to apply this method to an extensive series of skulls, when the opportunity arises, and would cordially invite others who are interested in craniology to do likewise."

Since that time Prof. T. Wingate Todd pointed out to the author that the akanthion point, through which one of the horizontal lines of demarcation was drawn, was very faintly shown in a large proportion of the Hamann Museum negro crania. He accordingly decided to make a survey of these crania in that museum, and as a result ascertained that the akanthion exhibited a remarkable amount of variation in its degree of development. That is to say, it was as well developed as in the white crania in a large proportion of cases, while in others it was very feebly shown indeed. After consultation with Prof. Todd, the writer decided to devise a new cranial point which he termed the subnasion (5). As a matter of fact, there was another cogent reason for the selection of the subnasion, namely, it was found to be essential for the purpose of devising the author's superior and inferior gnathic triangles (8, 9), which have been described elsewhere. Furthermore it will be necessary, for the above reasons, to substitute the subnasion for the akanthion in the author's naso-orbito-alveolar index (2) which was devised several years ago.

The other cranial points that were selected for the purpose of drawing the horizontal lines require a little discussion. The nasion, through which the uppermost line is drawn, is regarded by the majority of craniologists as a fairly satisfactory craniometric point, more particularly as it is capable of being readily located as a rule. The lower orbital margins, through which the second horizontal line is drawn, required much more careful consideration, for their contour was found by the author (3) to vary with age and sex in all the cranial groups that were studied. It would therefore be found advisable to confine a research of this nature not only to adult crania, but also to one sex at a time. An additional difficulty also cropped up. Thus it was ascertained that in many crania the right and left lower orbital margins were not quite on the same horizontal plane, in which case the mean of these levels had to be taken.

A difficulty arose with regard to the alveolar point. The author has always been accustomed to accept the definition of the latter as the most anteriorly projecting point on the alveolar margin of the upper jaw between the central incisor teeth. This is the form given by Duckworth (10), Thomson (11) and in Quain's *Anatomy* (12). This is the point through which the lowest horizontal line was drawn in the crania illustrating this memoir. It is only right to say, however, that Pearson (13) and Wood-Jones (14) describe the alveolar point as the lowest point in the mid-line of the upper alveolar border, which would necessarily be on a slightly lower level than that indicated by the previous definition.

Procedure. All the photographs of the crania of modern Man and the casts of fossil crania were made exactly life size. The author finds it difficult to express in really adequate terms his gratitude to Prof. Wingate Todd and Miss W. M. Kuenzel for the high technical skill they displayed in taking these. It was of course essential that the level of the camera lens with reference to the facial norma be exactly the same in all cases. Each specimen was there-

fore carefully orientated first of all in the Frankfort plane. The level of the camera was then adjusted, so that the centre of the lens was exactly on a level with that plane. Prof. Todd and the author marked on each photograph the positions of the nasion, the lower orbital margins, the subnasion and the alveolar point. The horizontal lines through these were then very skilfully drawn on the photograph by Miss Kuenzel.

It will be noted from the accompanying photographs that the three zones thus mapped out involve the vertical area of the face included under the term "facial height," as measured from the nasion to the alveolar point. That is to say, the author has no intention of dealing with the area above the level of the uppermost line, which might be termed the frontal area. As a matter of fact, the vertical dimension of this area presented no material racial difference, when studied for example in the Hamann Museum white and negro crania. At first sight this seemed to be a startling statement to make. The explanation was that the extreme summit of the photograph in the case of the negro crania was found to be situated well back in the parietal region, whereas in the white crania it was situated much further forward. The result was, that the amount of expanse of skull displayed by the upper portions of the photographs exhibited no definite racial difference in these two cranial groups.

The author was thus compelled to limit the investigation to the three horizontal zones indicated above. He will therefore refer to these throughout this paper as the upper, intermediate and lower zones of the facial norma. It had better be stated at this stage that the present paper is to be regarded strictly as of the nature of a preliminary communication, though its possibilities are immense. It is obvious that a thorough investigation of the whole subject would take years to complete. Besides, the expense would necessarily be very great, as photographs of hundreds of crania would have to be taken, in order to strike an average for each racial type. So far as the author knows, the Hamann Museum is the only place where such an investigation could be carried out. There the investigator will find a most complete and up-to-date equipment, as well as a courteous and obliging staff from the chief downwards, who are always ready to furnish help and encouragement to every worker.

HORIZONTAL ZONES OF THE FACIAL NORMA IN MODERN MAN

These three zones are displayed very successfully in the male white skull shown in Plate 1, fig. 1. It will be noted that the upper zone is by far the largest in vertical dimension. The intermediate zone also happens to be intermediate in size, while the lowest zone is the smallest of the three. The writer found that the upper zone reached its greatest vertical dimension in the higher races of modern Man, and, moreover, ascertained that it was associated with the high orbital apertures which are the general rule in these racial groups. This impression was confirmed by a study of this zone in the Mongolian

races, in which, as is well known, the average height of the orbital aperture reaches its maximum. For instance, the writer was privileged to study this zone in the Eskimo and Mongol crania of the United States National Museum and also in the Eskimo crania of the Canadian Arctic Expedition, 1913–18, in all of which the orbital height and the height of the upper zone reached their maximum dimensions. That is to say, these Mongolian types both showed higher maxima than even the Hamann Museum white crania.

The slight disproportion between the vertical dimensions of the intermediate and lower zones, which was found to exist in the Hamann Museum white crania, became greatly lessened in the Eskimo and Mongol crania. Indeed, in a large proportion of the crania representing the latter racial types, the vertical dimensions of these two zones were almost exactly equal. This racial feature was found to be due, not so much to a reduction in the vertical dimension of the intermediate zone, as to an increase of the subnasion-alveolar height in these Mongolian races. This impression was confirmed in a recent research by the writer (6), as a result of which he ascertained that the average subnasion-alveolar height in these male Eskimo crania was 16·9 mm. and in these male Mongol crania 18·4 mm., as contrasted with only 15·7 mm. for the Hamann Museum male white crania.

The zones on the facial norma of the native Australian skull formed a decided contrast to those exhibited by the white and the Mongolian races. For example, it will be observed that in the skull of the Australian aboriginal shown in Plate 2, fig. 3, the vertical dimensions of the upper and the intermediate zones had become very nearly the same, though the dimension of the upper zone was still slightly the larger of the two. The explanation of this change was found in a study of the orbital height in this racial type. It is of course a well-known fact that the latter dimension is definitely less on the average in the aboriginal Australian than in the white and the Mongolian races. It was ascertained that a reduction of the height of the orbital aperture produced a slight raising upwards of its lower margin. Such a change would naturally tend to equalise the vertical dimensions of the upper and intermediate zones of the facial norma. The author discovered, however, that there was a second factor which helped to increase the vertical dimension of the intermediate zone in the black races. This was a slight lowering of the level of the subnasion. As the horizontal line mapping off the intermediate zone inferiorly is drawn through this point, the effect is of course obvious. It is important to direct attention at this point to this lowering of the level of the subnasion in these races.

If the Australian and Tasmanian crania represented in Plate 2, figs. 3 and 4, be studied, it will be noted that they exhibit a peculiar doubling of the lower edge of each lateral half of the nasal aperture. This produces a peculiar shallow groove known as the "Simian gutter." This appearance, it may be added, was also exhibited by most of the Hamann Museum male negro crania. It is rather interesting to note that the Rhodesian and La Chapelle skulls also

show this Simian gutter (see Plate 4, fig. 7 and Plate 3, fig. 5). The writer was unable to detect it in any of the Hamann Museum male white crania. Certainly Plate 1, fig. 1 shows no sign of it. This Simian gutter has the effect of causing each lateral half of the lower edge of the nasal aperture to extend to a more inferior level than in the white races. It is obvious, however, that the lower edge of the gutter is always below the actual level of the floor of the nasal fossa, and must therefore of necessity also be slightly below the level of the subnasion (5).

These impressions were confirmed by a study of these zones in the skull of a race akin to the native Australian, namely the Tasmanian aboriginal. This racial type is shown in Plate 2, fig. 4. It will be noted that in this specimen the vertical dimensions of the superior and the intermediate zones are almost exactly the same. It was indeed a privilege to be enabled to study this interesting racial type, for it was evident that the Tasmanian skull exhibited a further stage of the action of the two factors referred to in connection with the Australian skull. Thus it was significant to note that the Tasmanian race exhibits the lowest average for the height of the orbital apertures of his skull among the races of modern Man, excluding of course the dwarf races. The result of this was of course to produce a slight raising upwards of their lower orbital margins. This Tasmanian skull also exhibited a very low subnasion, but it is naturally impossible to say whether or not this is a characteristic feature of Tasmanian crania in general. It may be added that the arrangement of the zones in two Melanesian skulls belonging to the author conformed exactly with those found in the Australian and Tasmanian crania. The zones in the Hamann Museum negro crania were also found to correspond to those found in the other members of the black races, though the characteristic equalising of the vertical dimensions of the upper and intermediate zones was not so marked as in the Tasmanian skull.

It is rather remarkable to note the striking reduction in the vertical dimensions of the lower zone in the Australian and Tasmanian crania shown in Plate 2, figs. 3 and 4, when compared with Plate 1, fig. 1. The main cause of this naturally was the foreshortening in the photograph, due to the marked condition of subnasal prognathism exhibited by these crania. Superadded to this was the slight lowering of the subnasion already referred to. This reduction of the lower zone certainly was a most pronounced feature of the photographs of the negro, Australian, Melanesian and Tasmanian crania, when compared with those of the Mongolian and the white races.

It was rather interesting to be able to record the fact that a condition like microcephaly did not apparently disturb the relative proportions of the three zones of the facial norma in the black races. For instance, the upper and intermediate zones in the well-known skull of a microcephalic Basuto woman still exhibited vertical dimensions almost exactly the same in extent. Similarly, the lower zone of this skull exhibited the marked reduction shown by the Australian and Tasmanian crania in Plate 2, figs. 3 and 4.

HORIZONTAL ZONES OF THE FACIAL NORMA IN FOSSIL MAN

These zones were studied in excellent casts of the Rhodesian, La Chapelle and Gibraltar skulls in the Hamann Museum. The results obtained will therefore have to be regarded as merely approximate, but it was evident that they portrayed the conditions existing in the actual skulls. The author was enabled to confirm this in the case of the Rhodesian and Gibraltar skulls.

The zones presented by the Rhodesian skull are displayed in Plate 4, fig. 7. A glance at this will show an appearance totally different from that presented by the racial types of modern Man that were available for study. For instance, it will be noted that the vertical dimensions of all three zones are almost exactly the same. The relative proportions of the upper and the intermediate zones conformed, however, to those displayed by the negro, Tasmanian and Australian crania. This was certainly a striking fact to have to record. It will serve as a contribution to the discussions regarding the exact position of Rhodesian Man in the human family tree. The vertical dimension of the lower zone was outstanding. Indeed, there was nothing to compare with it among all the modern crania that were accessible to the writer.

The author experienced difficulty in locating the nasion in the La Chapelle skull owing to a notch of bone having been broken away over the site of that craniometric point (see Plate 3, fig. 5). After consultation with Prof. Todd, it was decided that its approximate position was that indicated in the figure. The three zones displayed by this skull were quite remarkable when compared with their appearance in the crania of modern Man. For example, it was noted that the intermediate zone was definitely greater than the upper in its vertical dimension. This, of course, was an exact reversal of the condition found in the white and the Mongolian crania. Indeed, it was impossible to compare the appearance as presented by this skull in Plate 3, fig. 5, with that of any known type of modern Man. The lower zone was very much reduced in this skull, as one would expect in one exhibiting such an extreme degree of prognathism.

When the author came to study the three zones in the Gibraltar skull, he was rather interested to find that they presented an appearance strikingly similar to that displayed by the La Chapelle skull. It was certainly remarkable to be able to record the fact that the zone in these two crania, representative of the European type of Neanderthal Man, agreed so closely. This was all the more noteworthy in view of the fact that the pattern they displayed was totally different from that of any racial type of modern Man known to the writer. As this paper is strictly a preliminary communication, it will not be advisable to pursue any further discussion on this matter at present.

PROBLEMS SUGGESTED BY THIS PAPER

The cranial material at the author's disposal, small though it was, suggested that these three zones of the facial norma displayed some degree of racial consistency. For instance, in the white and the Mongolian races the upper zone exhibited by far the greatest vertical dimension, while the much smaller intermediate and lower zones tended to approximate to one another in vertical height, particularly in the Mongolian types (Eskimo and Mongol). In the case of the Hamann Museum white crania the vertical dimension of the intermediate zone was slightly greater than that of the lower zone in the majority of cases.

On the other hand, in the black races, as represented by the Hamann Museum negro, the native Australian, the native Tasmanian and the Melanesian, these three zones presented a totally different pattern. In these four racial types the upper and intermediate zones tended to be of approximately the same height, while that of the lower zone was reduced in a remarkable degree, chiefly due to foreshortening in the photograph produced by prognathism. It was thus evident that this three-zone system was capable of dividing the races of modern Man into two great groups, as indicated above.

One great purpose of the author in writing this paper was to direct the attention of the younger generation of craniologists to a line of research that would probably bear rich fruit. For example, an investigation into the relative degree of growth of these three zones of the facial norma during infancy and adolescence would prove a profitable field of inquiry. In relation thereto the author would suggest two important factors that must certainly be considered, namely, the growth of the maxillary antrum and the development of the upper dental arcade. Both of these have an influence upon the evolution and growth of the maxillae that is paramount. The growth and expansion of the nasal fossae would of course also require consideration. As already mentioned in an early part of this paper, each sex would require to be considered separately, in view of the important influence of the sexual factor upon the orbital apertures (3), the nasal index (7) and the gnathic index (4), which has been fully discussed by the author in previous papers.

In order to emphasise still further the great possibilities indicated by a study of these three facial zones, the author wishes to point out that three new cranial indices could be produced by comparing the proportion which the height of each of the zones bears to the total facial height. Moreover, three more would result from a study of the proportion which the vertical dimensions of the three zones bear to each other.

CONCLUSIONS

1. This is the first time, so far as the author can ascertain, that an attempt has been made to divide the facial norma into horizontal zones.

2. These are mapped off by horizontal lines passing through the nasion,

the lower orbital margins, the subnasion and the alveolar point. By this means three horizontal zones are mapped off, namely upper, intermediate and lower.

3. It was found that this three-zone system was capable of dividing modern Man into two main groups.

4. The first group was found to consist of the white and the Mongolian races. In these the upper zone exhibits by far the greatest vertical dimension. The intermediate and lower zones are much smaller, and tend to possess approximately the same height.

5. The second group was represented by the Hamann Museum negro, the native Australian, the native Tasmanian and the Melanesian. In these the zones presented a totally different pattern. In these four racial types the upper and intermediate zones tended to be approximately of the same height, while that of the lower zone was reduced in a remarkable degree.

6. The study of those zones in the crania of fossil Man, though it had to be made on casts of the original crania, yielded some remarkable results. In the Rhodesian skull the upper and intermediate zone tended to be approximately of the same height, as in the crania of the modern black races. The three zones in the La Chapelle and Gibraltar skulls displayed an appearance remarkably alike, and totally different from that of any racial type of modern Man known to the writer.

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EXPLANATION OF PLATES

Plate I

Fig. 1. Horizontal zones of the facial norma in a Hamann Museum male white skull.

Fig. 2. Horizontal zones of the facial norma in a male Eskimo skull (Victoria Museum, Ottawa). Note that the pattern corresponds to that shown in fig. 1.

Plate II

Fig. 3. Horizontal zones of the facial norma in an aboriginal Australian skull (Hamann Museum).

Fig. 4. Horizontal zones of the facial norma in an aboriginal Tasmanian skull (Hamann Museum). Note that the pattern corresponds to that exhibited by the aboriginal Australian skull.

Plate III

Fig. 5. Horizontal zones of the facial norma in a cast of the La Chapelle skull.

Fig. 6. Horizontal zones of the facial norma in a cast of the Gibraltar skull. Note that the pattern corresponds to that shown by the La Chapelle skull, and is different from that displayed by the racial types of modern Man.

Plate IV

Fig. 7. Horizontal zones of the facial norma in a cast of the Rhodesian skull. Note that the pattern is different from that presented by the racial types of modern Man.

Fig. 8. Horizontal zones of the facial norma in the well-known cast of the skull of a microcephalic Basuto woman. Note that the pattern conforms to that exhibited by other members of the black races (see Pl. II, figs. 3 and 4).

Fig. 2. Eskimo skull.

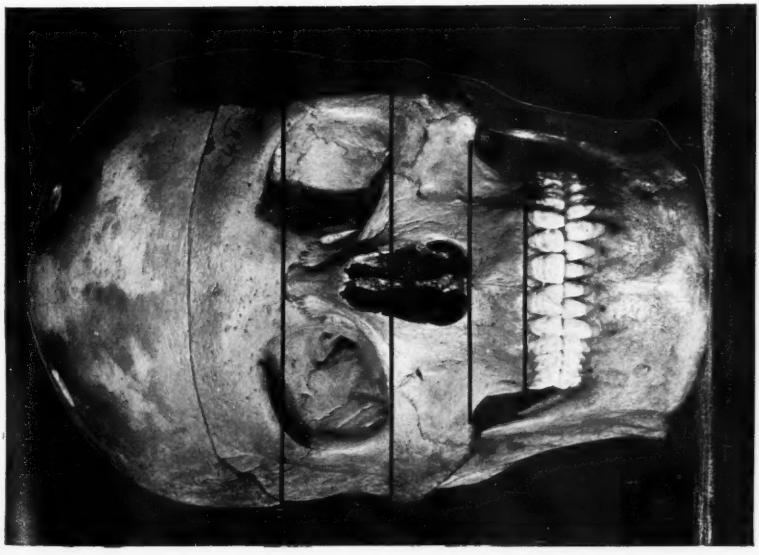

Fig. 1. Male white skull.

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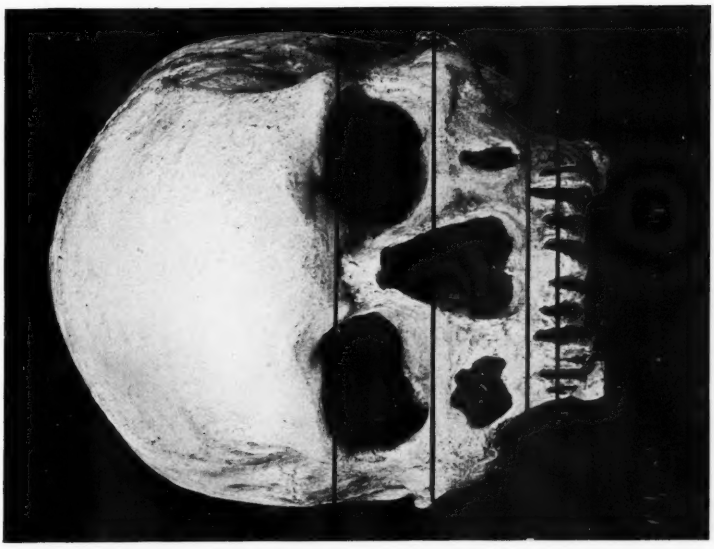

Fig. 4. Aboriginal Tasmanian skull.

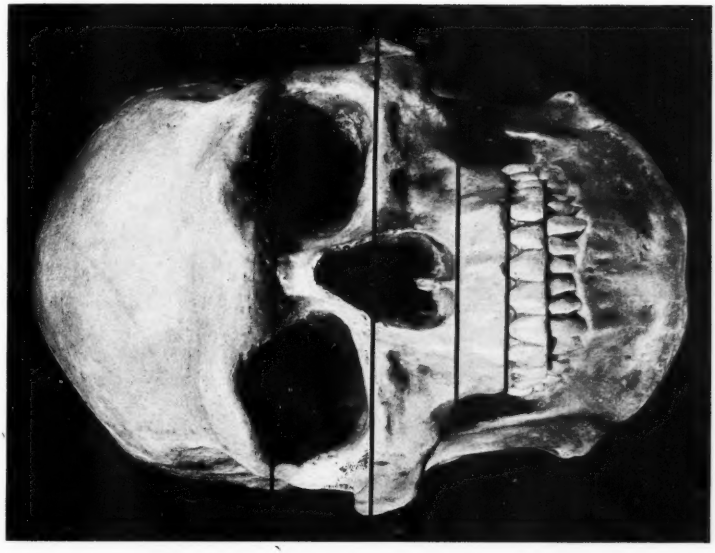

Fig. 3. Aboriginal Australian skull.

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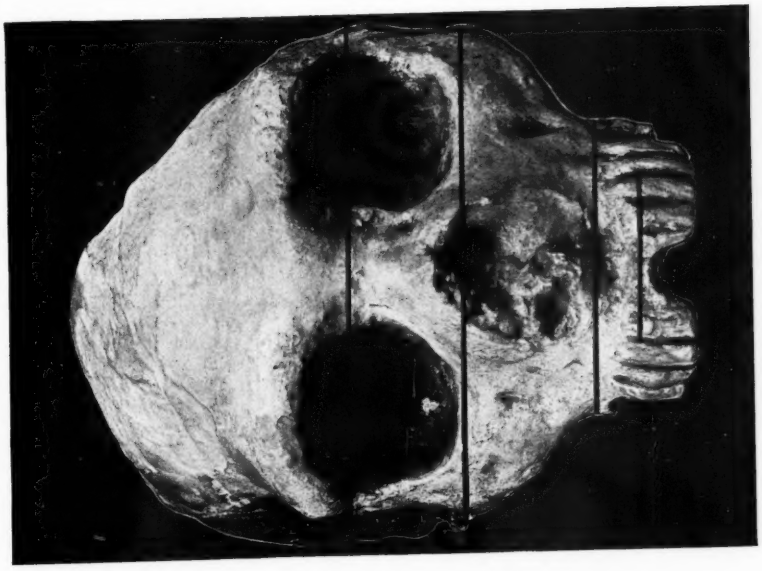

Fig. 6. Gibraltar skull.

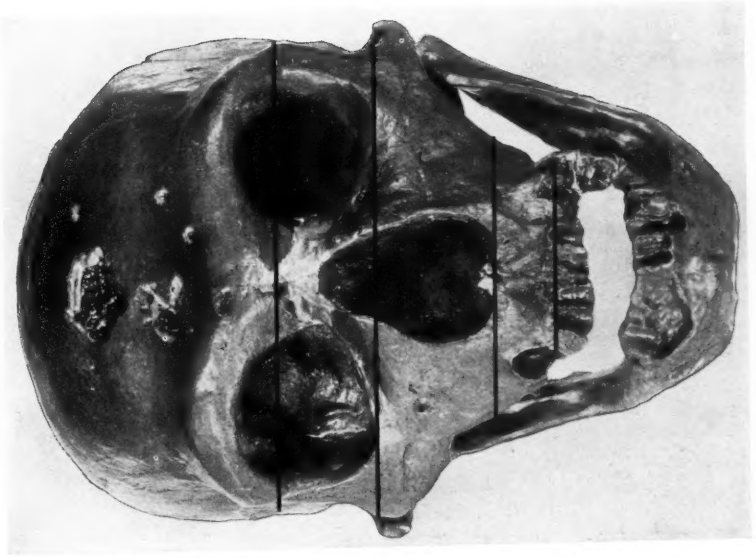

Fig. 5. La Chapelle skull.

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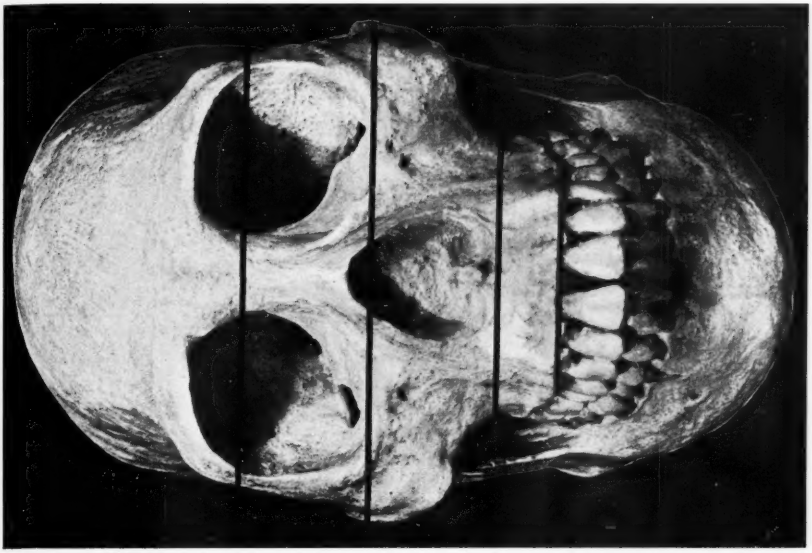

Fig. 8. Basuto skull.

Fig. 7. Rhodesian skull.

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NOTE ON THE RELATIVE LENGTHS OF FIRST AND SECOND TOES OF THE HUMAN FOOT

By Major-General BRUCE MORLAND SKINNER,
C.B., C.M.G., A.M.S. (Retired)

Many years ago when a number of recruits was passing under physical examination, it became notable that their feet might be classed under two heads, with regard to the prominence or otherwise of the great toe in relation to the second. Some years later, being in another recruiting centre for a short time, the above condition was noticed again, and tabulated as follows:

Number of recruits	1st toe longest	2nd toe longest	1st and 2nd toes equal
323	175	74	74

On finding these notes amongst my papers after a long interval a visit was paid to the Natural History Museum in London, and the following observations were made upon the skeletons exhibited there:

	1st toe longest	2nd toe longest	1st and 2nd toes equal
Caucasian, F.	—	—	R. and L.
Caucasian, M.	—	R. and L.	—
Arawak, M.	—	L.	R.
Arawak, F.	—	R. and L.	—
Negro	R.	—	L.
Negrillo, F.	R. and L.	—	—
Mincopee, M.	—	R. and L.	—
Tasmanian, M.	—	R. and L.	—
Specimen, rt. leg	—	R.	—
Articulated skeleton, Man, with horse	—	L.	R.

A visit was also paid to the Museum of the Royal College of Surgeons, and the following notes recorded, omitting such skeletons as were incomplete, and querying those specimens which appeared doubtful:

	1st toe longest	2nd toe longest	1st and 2nd toes equal
9 Europeans	6	2	1
1 American	1	—	—
1 Lapp	—	L.	R.
1 Egyptian	—	—	1
1 Fuegian	—	1	—
3 Peruvians	—	3	—
2 Peruvians	—	—	2
1 Arawak	—	—	1
1 N. Am. Indian	—	—	1
1 Eskimo	1	—	—
1 Iniue	—	1	—
1 Tahiti	—	1	—
2 Java	—	2	—
1 Japanese	—	1	—
1 Aino	—	—	1

	1st toe longest	2nd toe longest	1st and 2nd toes equal
1 Bhutani	—	1	—
1 Malay Arch.	—	1	—
2 Chinese	—	2	—
1 Samoyede	—	1	—
2 Sikh	—	2	—
1 in same case as giant Byrne	—	1?	—
1 New Hebrides	—	1	—
1 Andamanese M.	—	—	1
1 Andamanese F.	—	1	—
2 Negro	1?	—	1
1 Balumba	—	1	—
3 Bushman	—	3	—
2 Madagascar	1	1	—
2 W. Australia	—	1?	?
2 Australia	—	2	—
1 Tasmanian	R.	L.	—
1 Tasmanian	—	1	—

Unfortunately, as now situated it is impossible for me to compare my observations with those which have been published by other observers. I hope that my data will prove of use to some future enquirer. Meantime it is clear that in the British recruits examined by me the first toe is usually longer than the second (54 per cent.), whereas, if I may judge from the skeletons of African, Asiatic and American native races represented in our museum collections, the second toe is usually the longer. The longer second toe may be regarded as the persistence of a simian feature which has disappeared from a large percentage of white people. Why this change has taken place is a matter for further enquiry.

It may be of interest for readers to know that in the 323 recruits examined 16 had supernumerary nipples, 10 men on the right side, 5 on the left, and 1 on both sides.

APPOINTMENT

Dr R. Gaskin Inkster has been appointed to the Chair of Anatomy in the University of Manitoba, as from 1 October, 1931. Prof. Inkster graduated in Medicine at Edinburgh University in 1922, wherein, after a year's post-graduate hospital work, he spent a twelvemonth or more as Demonstrator in Anatomy under Prof. Arthur Robinson. In October, 1924, he relinquished his Edinburgh appointment to take up a Demonstratorship in the Anatomy Department of Leeds University, holding that post until his present appointment and therein developing his interests in Embryology and the elaboration of various injection techniques. In 1927 he submitted a thesis for the degree of M.D. upon "The Form of the Talus, with special reference to that of the Australian Aborigine"; for which work (at present unpublished) he was awarded a gold medal.

REVIEWS

The Teeth, the Bony Palate and the Mandible in Bantu Races of South Africa. By J. C. Middleton Shaw, M.A., B.Dent. Sc. (Dub.), D.D.S. (Johannesburg), F.I.C.D. (London: John Bale, Sons and Danielssen, Ltd.) 1931. Pp. xvi + 134. 54 figs., 66 tables. 12*s.* 6*d.* net.

The reproach that anatomists have done little to disperse the "dental darkness" of modern Man, a reproach all the more surprising since teeth have ever been the corner stone of palaeontology and comparative anatomy, is indeed mitigated by such studies as the above. The opportunity given by geographical position has been embraced by the Dental Schools of our Overseas Universities, and in the last few years at least two important monographs have appeared devoted to the teeth and other cognate matters in primitive races. Dr Campbell, of the Dental School of the Adelaide University, produced his valuable study of the teeth of the Australian aboriginal a few years ago, and now Dr Shaw, of the Dental School of the Witwatersrand University, has followed with his study of the same anatomical field in the Bantu races of South Africa. In the one case we have a race, long isolated, comparatively homogeneous, and reputed to be the most primitive of existing peoples; in the other, a race that has established itself only recently in its present home, most probably of mixed origin, and of a semi-civilised status.

Dr Shaw has wisely followed the methods of Dr Campbell and always, when possible, brought his study into conformity with the plan followed by the earlier author. The subject gains much from this parallelism. The results indicate that as we have passed from the uncivilised, through the semi-civilised, to our present civilised state, our teeth have become progressively smaller, irregularities, anomalies and variations more abundant, and finally, dental caries and alveolar affections universal. The history of teeth and the associated structures is an inverted progress; it is a progressive reduction of masticatory efficiency. In the Australian, under his own conditions, caries is rare, occurs only in old age, and then only when attrition has exposed the pulp cavity.

In addition to the descriptive morphology and the mensuration of the teeth, the authors include an analysis of the palate, the mandible, etc. The story here is the same as in the case of teeth. Further, the variations are collected and an attempt made to analyse these by comparison with the teeth of the Primates and fossil Man. For instance, Dr Shaw has studied the problem of taurodontism in the Bantus and others, and, rather surprisingly, discovers a high frequency of this condition in the Boskopoid race. One reason, and probably the most important, for excluding Neanderthal Man from the ancestry of modern Man is the presence of hypertaurodontism in his teeth. This opinion was fortified by Dr Campbell in his study of the Australian, for not only did he find no taurodontism but produced evidence from the conformity of the teeth and the arrangement of the occlusal pattern, etc. that they were more primitive, i.e. closer to the Primate form than any other teeth examined. Dr Shaw's results open up the whole question again.

The enquiry is pushed into the region of social anthropology, and the meaning, extent, and distribution of tooth mutilation and extraction are dealt with. In Africa the distribution is from the centre toward the eastern coast, while it is absent in the west and south. In Australia the custom is said to be absent in the north and the centre while present in the southern periphery. The results obtained from these

enquiries would appear to be equally palatable to the diffusionists, the isolationists, and the psycho-analysts.

The author meditates on the bearing his results have on dental practice. Though more restrained than Dr Campbell, yet his conclusions are the same. Civilisation has given us dental caries and dentists. Dr Campbell would sweep aside vitamines and the rest and insist that dental perfection can only be obtained in the same manner as the Australian got it—a diet almost raw, generally gritty, and always coarse.

The monograph is interesting throughout; it is thoroughly done, put together in an attractive manner, and adequately illustrated. As Sir Arthur Keith remarks in his foreword—Dr Shaw's work does lessen the scientific gloom that envelops the anatomy of the teeth of modern Man.

Toldt, Anatomischer Atlas. 15th edition, revised and edited by Prof. F. HOCHSTETTER. (Urban und Schwarzenberg, Berlin and Vienna, 1931.)

Bd. I. Die Gegenden des menschlichen Körpers, Das Skelettsystem, Das Muskelsystem. Figs. 1–686. Geh. RM. 24; geb. RM. 27.

Bd. II. Das Darmsystem, Das System der Harn- und Geschlechtswerkzeuge, Das Gefasssystem. Figs. 687–1208. Geh. RM. 23; geb. RM. 25.50.

Bd. III. Das Nervensystem, Die Sinneswerkzeuge. Figs. 1209–1599. Geh. RM. 16; geb. RM. 18.

The appearance of the 15th edition in thirty-one years of Toldt's well-known *Atlas* bears witness to the usefulness of the work and to the continued vitality of its editorship in the hands of Prof. Hochstetter, who has been responsible for the last four editions. It is pleasing, in these days of expensive and over-elaborate methods of reproduction, to note the popularity of an atlas which still relies almost entirely on wood-cuts for its illustrations. These are all well executed; some reach a high level of excellence, particularly the beautiful illustrations in vol. I of the internal architecture of bones. In this edition some entirely new figures have been added, and others have been modified or replaced.

Detailed criticism of a work of this standing is quite uncalled for. One is glad to note the increased attention paid to illustrating developmental anatomy. The relatively few but useful histological pictures might perhaps be supplemented, without departing from the general scope of the work. The only section which receives inadequate treatment is the lymphatic system: no attempt is made to illustrate the lymph drainage of any of the viscera, except for an old picture of the mesenteric lymphatics injected with mercury.

Special mention must be made of the excellent series of X-ray photographs, prepared by Dr Josef Palugyay, which are the only exceptions to the use of wood-cuts. There are thirty-seven plates of the joints, and twelve of the viscera, all well chosen and beautifully reproduced, except one too densely printed picture of the foot. The scale of reproduction is commendably large. The plates are entirely free from disfiguring pointers; instead, a fully labelled tracing of each plate is placed opposite to it.

The chief feature of this edition is the introduction of the revised terminology proposed by the nomenclature committee of the Anatomische Gesellschaft in an interim report issued in 1929. British anatomists, who are at present engaged in an attempt of their own to amend the B.N.A., will examine with special interest the changes proposed in Germany. Unfortunately, the revisers in the two countries have worked on very different lines. The main feature of the German revision is the alteration of terms of relative position: *anterior* and *posterior*, *superior* and *inferior* have been removed with laboured thoroughness; *medial* and *lateral* have almost entirely disappeared from the limbs, but remain in the head and trunk. The result, in many instances, can only be described as pedantic. An *art. thyreoidea caudalis* or an *art.*

glutaea cranialis sound, literally, rather far-fetched; the superior and inferior rectus muscles of the eyeball are called *tegmentalis* and *maxillaris*, while the medial and lateral muscles are unaltered; the semicircular canals are called *occipitalis*, *parietalis* and *lateralis*; the cerebral arteries become *oralis*, *media* and *aboralis*; the cerebellar arteries are *dorsalis*, *oralis* and *caudalis*; the four parts of the duodenum are described as *cranialis*, *descendens*, *caudalis*, *ascendens*; these are examples. In the limbs, to speak of the humeral epicondyles as *radialis* and *ulnaris* may be permissible, but *caput fibularis* and *caput tibialis*, as applied to the gastrocnemius muscle, are surely misleading. The anterior and posterior tibial arteries and muscles are called *dorsalis* (ant.) and *plantaris* (post.). There are also a number of alterations in main names. Some of these have much to be said for them, e.g. the substitution of *fibularis* for *peronaeus* throughout, and the reappearance of *arteria ilica interna* (with a curious alteration in spelling). But other new names have been applied with no regard for brevity at any rate, e.g. the middle meatus of the nose becomes *meatus conchae ethmoturbinalis majoris*, and the anterior horn of the lateral ventricle becomes *recessus frontalis partis lateralis ventriculi telencephali*. One reason for the different ideals in Germany and in this country towards a revision of the B.N.A. seems to be that English names can usually be found which closely resemble the Latin ones, whereas the native German names are more usually quite different from the Latin terms.

But criticisms of terminology are not criticisms of the atlas which embodies them; indeed, one must award praise to the publishers for their public-spirited action in trying out the suggested alterations, for thereby can these be most effectively put to test.

In conclusion, this work may be specially recommended to students who wish to acquire a good German anatomical vocabulary. The simple-worded legends to the figures, the frequent use in close proximity of Latin and German terms, the full indexes, German and Latin, provided for each section, all help to make the atlas serviceable in that way, in addition to its usefulness as a collection of 1599 illustrations of human anatomy.

Studies on the Structure and Development of Vertebrates. By Edwin S. Goodrich, M.A., D.Sc., LL.D., F.R.S., Linacre Professor of Zoology and Comparative Anatomy in the University of Oxford. (London: Macmillan and Co., Ltd.) 1930. Pp. 837. 754 figs. Price 36*s*.

A close scrutiny of this work has given the reviewer complete satisfaction; it represents the last traditions of comparative anatomy—the traditions we associate with the names of Huxley and of Gegenbaur. And what an undertaking it is to write to-day a text-book which will summarise adequately and succinctly all that has been done in the realm of Vertebrate Morphology in these recent years! The literature which has to be mastered and assimilated is enormous. Prof. Goodrich's bibliography has 1186 references, and these are only the titles of the chief works he has utilised in writing this book. Behind all the information he has derived from published works lie his own researches. There are few systems of the vertebrate organisation Prof. Goodrich has not investigated at first hand. His text-book represents a successful synthesis of what he has observed himself tempered and augmented by what has been observed by other reliable workers.

Prof. Goodrich, in his title page, speaks of his book as "studies"; but in reality it is a systematic treatise on the comparative anatomy of vertebrate animals—a book for professional students of zoology and for teachers of comparative anatomy. It is a modernised and up-to-date Gegenbaur. It differs from Gegenbaur in that the facts which are cited and used as a basis for inference are drawn from enquiries into the manner in which animals develop rather than from investigations of their adult anatomy. For many a day this will certainly be the standard text-book on Vertebrate

Morphology in the English language. It is richly illustrated, and the illustrations in every instance are wisely chosen and help to elucidate the text.

Manifestly it would be impossible to give an adequate review of this text-book; one might as well attempt to pass judgment on a dictionary. It will be sufficient to note the order in which Prof. Goodrich takes up the various parts of the vertebrate body and the space he devotes to each system. Chapter I, occupying 86 pages, is devoted to the skeleton of the trunk—vertebrae, ribs and sternum. Chapters II, III and IV are allotted to a consideration of outgrowths from the trunk for purposes of locomotion—median fins and paired limbs—with the girdling structures—which serve as fulcra from which the limbs act. These three chapters occupy 126 pages. The five chapters which follow—chapters V, VI, VII, VIII and IX—are devoted to a consideration of the region of the head and are given 294 pages. The importance now attached to the morphology of the head region will be thus realised. The head region is dealt with in the following order. Its segmentation is discussed and then the cranium is considered. There follows a description and discussion of the skeletal elements derived from the visceral arches and labial cartilages. The middle ear and auditory ossicles are given a separate chapter. A chapter on the visceral clefts and gills completes the section of the book devoted to a consideration of the head. The vascular system and heart supply materials for chapter X (71 pages); the air bladder and lungs for chapter XI (34 pages). Chapter XII is devoted to the subdivisions of the coelom and diaphragm (44 pages), while chapter XIII covers that complex of structures which are connected with urinary and reproductive functions—a long chapter of 62 pages, but considering the intricacy of the parts concerned really a triumph of condensation. The final chapter, XIV, is devoted to the peripheral nerve system and sense organs and runs into 67 pages—rather an inadequate allowance for systems of so high importance. The central nervous system has been purposely omitted; indeed the word "brain" does not occur in the index. One feels that part of the book devoted to the morphology of the skull might have been profitably curtailed to leave space for a consideration of what after all is one of the most important of vertebrate organs.

Die normale Entwicklung des Knochensystems im Röntgenbild. Von Dr E. Ruckensteiner. (Vienna: Georg Thieme.) 1931. Pp. v + 79. RM. 18.60.

This volume by Dr Ruckensteiner of Vienna is the 15th volume in the series of Practical Manuals of Radiology, published by Georg Thieme of Leipzig. The book deals in masterly fashion with the developmental pattern of the osseous system and serves as a useful connecting link between that knowledge of primary centres of ossification which is usually limited to the field of the human embryologist and that knowledge of the child and the adult which is acquired in the radiological clinic.

The sections of the book deal with the whole skeleton in strict anatomical order: vertebral column, thorax, skull, teeth, upper limb and lower limb. The sections dealing with the limbs are of extraordinary interest from the point of view of age changes in the radiographic appearance. The difficulties associated with abnormal ossicles in the carpus and tarsus, pseudo-epiphyses and sesamoid bones are clearly depicted. The main virtue of the book consists in five charts, printed in colours, depicting by curves the range of variation in the time of appearance and union of the various secondary centres of ossification. These charts are invaluable, and furnish the first clear exposition of the wide range of variation in the dates of appearance of the ossification centres whilst at the same time stressing the inherent constancy of the pattern and order of development. The charts may be purchased separately, and as wall diagrams in the clinic or laboratory they serve as a ready check on those observations which are regarded as abnormal when they are really but examples of the normal range of variation. We safely recommend these curves to any anatomical or radiological department.

Normale Anatomie des Kopfes im Röntgenbild. Von KARL GOLDHAMER. (Vienna: Georg Thieme.) 1931. Part I, pp. x + 115, plates 1–15*a*; Part II, pp. ix + 44, plates 16–87*a*. RM. 120.

It is a common experience to return to the radiogram after intra-cranial exploration and to see clearly depicted thereon pathological landmarks which had escaped the eye of the observer. Areas of calcification in the meninges, areas of absorption or deposition of bone in the skull, changes in the choroid plexus and changes in the brain substance can so frequently be seen on the radiogram only after exploratory operation or autopsy. This indicates that our knowledge of the radiographic appearance of the skull is inadequate, and neither improved radiographic technique nor stereoscopic radiograms have been sufficient to compensate for our lack of knowledge of even the normal range of variation in the bones of the cranium and face.

These two volumes by Karl Goldhamer of Vienna deal with the normal anatomy of the skull as seen by X-ray. The first volume is devoted to the normal lateral and antero-posterior views, whereas the second volume deals with those particular oblique and asymmetric views which have been called into being by the requirements of the dental surgeon, aural surgeon and the exponent of the cranial air sinuses.

The standard radiographic views of the dried skull serve as an introduction to the gross anatomy. The radiograms, printed on glossy paper, are accompanied by transparent keys on which all structures are numbered. The printed key gives the anatomical equivalent in German, English, French and Spanish. The radiograms of the dried skull are followed by those of the living subject and the differences due to the absence of presence of the soft structures are well illustrated.

The second volume gives a series of more or less standardized oblique views which serve for the detailed examination of those areas and structures which prove to be so elusive in the normal standard views of the skull. The temporal bone, the pneumatic sinuses, the structures in relation to the base of the skull and the teeth are illustrated in great detail, especial attention being given to those views of the skull which are associated with the names of so many radiologists.

The photographic reproductions of the dried skull are of extreme beauty. Some of those of the living subject might be improved. In view of the fact that so many of the structures which vary considerably with age are so well depicted it is strange that the age and sex of the subject has not been stated. Age is of such importance in assessing the extent of departure from normal when dealing not only with teeth but also with bone texture, sutures, Pacchionian granulations and venous canals in the diploë. These factors are of considerable importance in the interpretation of the radiographic appearances of the skull conditions of increased intracranial pressure and in cases of primary or secondary tumours of the skull bones. For students of anatomy, neurology and radiology the radiograms of the dried skull fulfil a definite need and may be recommended as useful books of reference.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

November, 1930 *February*, 1931
May, 1931 *June*, 1931

RECORDED BY
R. J. GLADSTONE

EDITED BY
E. BARCLAY-SMITH

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

NOVEMBER, 1930

THE Annual Meeting of the Society was held at St Thomas's Hospital, on 21 November, 1930. The President, Professor Bryce, in the Chair.

Dr J. H. MULLIGAN demonstrated specimens and read a paper on "A method of staining the brain for macroscopic study." The paper will be submitted for publication in the *Journal of Anatomy*.

Professor LE GROS CLARK called attention to the value of the method in the preparation of museum specimens and in demonstrating the white striae in certain areas of the cortex.

Dr C. LAMBERT ROGERS communicated a paper by Professor C. M. WEST and himself on "The true nature of the foramen of Magendie," which will be submitted for publication in the *Journal of Anatomy*.

Professor WEST called attention to the small size of the choroid plexus of the fourth ventricle as seen in their dissections.

Professor JOHNSTON corroborated the existence of the foramen of Magendie, but doubted whether normally it was so extensive an opening as had been described. By removing the floor of the ventricle, and examining the roof from the front, the choroid plexus, though small, could be quite clearly seen.

Mr J. B. HUME referred to the proof of the existence of the foramen in radiological examinations when air is injected into the ventricles of the brain.

Professor J. P. HILL communicated a paper by Dr T. T. FLYNN and himself on "Segmenting eggs of Monotremes." A series of lantern slides were exhibited, and a full account of their observations will be published later.

Mr J. WHILLIS read a paper on the lower end of the oesophagus of which the following is an abstract:

(1) There is no histological evidence of a cardiac sphincter in Man. The wall of the lower end of the oesophagus contains two coats of unstriped muscle.

(2) The cat shows a structure similar to that found in Man.

(3) In the cat and Man the oesophageal opening in the diaphragm is bounded in front by tendon and behind by the decussating fibres of the right crus. The intra-abdominal oesophagus is short.

(4) The oesophagus of the rabbit contains three coats of striped muscle in its wall. The striped muscle is sharply demarcated from the plain muscle of the stomach. There is a well-marked thickening of the circular muscle in the cardiac region.

(5) In the rabbit and guinea-pig the intra-abdominal oesophagus is long, and the opening in the diaphragm much larger than the oesophagus which traverses it.

(6) Radiological examination shows:

(*a*) That in Man the diaphragm, when contracted, constricts the lower end of the oesophagus, and that when the diaphragm relaxes there is no further obstruction to the passage of barium emulsion into the stomach.

(*b*) The diaphragm has an action in the cat similar to that in Man. In the rabbit it has no obvious action on the oesophagus.

(*c*) Section of both vagus nerves produces no obstruction of the oesophagus in the cat.

(*d*) Section of both vagus nerves in the rabbit produces spasm of the cardiac region of the oesophagus lasting for more than one hour.

Mr J. B. Hume asked if Mr Whillis considered that the lower six intercostal nerves supplied the diaphragm?—Mr Whillis thought that the lower intercostal nerves and also the upper lumbar nerves gave branches to the diaphragm, but doubted whether these were somatic in nature.

Professor Le Gros Clark referred to the observations of Graham, that fluid introduced into the oesophagus was retained there until the movement of swallowing was performed.

Dr Stibbe, Professor Blair, Professor Woollard and Dr Cave also took part in the discussion.

Dr D. Rioch made a communication on "The centre median nucleus of Luys," which will be published in the *Journal of Anatomy*.

Professor Le Gros Clark, in congratulating Dr Rioch on his confirmatory evidence for the establishment of the homology of the centre median nucleus in the mammalian thalamus, said that he had no doubt that this interpretation was correct. His own studies of the thalamus of *Tarsius* and of the thalamus of several species of the Lemuroidea showed that this nucleus was certainly developed in the caudal part of the internal medullary lamina and in close association with the nucleus of the habenulo-peduncular tract. As regards the suggestion made by some authorities that the centre median nucleus represents the Nucleus rotundus of lower Vertebrates, he believed that a comparative study of the former in different Mammals was against this view.

Mr A. Ralph Thompson described a case of "Pregnancy without an apparent vagina," of which the following is a summary.

R. P., a girl aged twelve years, was seen by me at the end of January, 1930. She was well developed, and the mother stated that she had had the condition since birth.

There was a small hole situated in the front part of the region of the labia minora. Through this hole urine was discharged. There was no vagina apparent. The labia majora were fully developed and normal in appearance.

I operated upon the case, and after the operation I was speaking to Mr Gibberd, the obstetric registrar at Guy's Hospital, and he told me that only a short time before our conversation he had done a Caesarean section on a woman in whom no vagina was to be seen. There was, however, a small hole through which urine was discharged.

A living baby was delivered by the Caesarean section, and the woman did well.

The case which came under my care explains, in all probability, the nature of the lesion.

At the operation I slit the conjoint labia minora and exposed the vagina, which lay in its usual position, and was normal in appearance, save that there was no very obvious hymen.

At the time of the operation I was not very clear as to the exact position of the urethra.

After the conjoint labia had been divided, I excised on each side a good deal of mucosa, so as to be sure that there should be no reunion.

A dressing was secured with sutures on the edges of the excised mucosa. Every precaution was taken against bleeding. Nevertheless about a week after the operation she had a smart haemorrhage which continued for some days, and gradually subsided, until on the fifth day there was no haemorrhage.

I was inclined to think that the bleeding may have come from the uterus, and may have been a menstruation.

The girl has not had any further bleeding.

She did well after the operation, and I saw her again on 5 March, but it was not clear at this time what was the position of the urethral orifice, but on 13 October the condition was quite evident.

The urethra is present, and is in the usual position.

The vagina is normal in appearance and position.

I take the case to be one of conjoint labia minora, in the front part of which the orifice of the urethra lay having the same opening as the vagina.

Through this hole blood might have been discharged at future menstrual periods, and in view of Mr Gibberd's case, it is not impossible that pregnancy might occur. I do not think this point need be laboured further.

That such a deformity is not incompatible with a pregnancy makes the case one of forensic interest, as well as one of anatomical importance.

The condition I have described may be common, but I have only seen it once, and thought a note on it might interest the Society.

Mr A. Ralph Thompson also communicated a paper on the "Clinical Anatomy of the Urinary Tract."

Professor Frazer showed lantern slides of sections through a young human embryonic shield. The specimen, a tubal pregnancy, was removed by operation, and put at once into preservative fluid. The histological condition was good, but the embryonic layer had unfortunately been ruptured, perhaps before fixation. The shield, in consequence, was markedly convex upwards in all directions: its antero-posterior length was approximately 0·5 mm. A well-formed head-process projected forward for a few sections in front of the anterior end of the ectodermal thickening of the streak, and apparently terminated in a definite end-plate of mesodermal nature. Unfortunately sections here were tangential and difficult to interpret. The head-process had a definite lumen, or chordal canal, with large cells radially disposed round it, and it appeared to be continuous with mesodermal layers on each side. Entoderm was attached to its lower aspect, which was complete.

Professor J. P. Hill and Professor Waterston took part in the discussion.

FEBRUARY, 1931

AN ordinary meeting of the Society was held on Friday, 6 February, at the Medical School, Guy's Hospital, Professor Mary Lucas Keene, Vice-President, in the Chair.

Professor T. B. JOHNSTON showed a specimen of partial duplicity of the notochord in an 11 mm. human embryo, an account of which will be submitted for publication in the *Journal of Anatomy*.

Professor FRAZER stated that he had seen a similar case in a human embryo. The notochord divided far back into two. The two chords passed forward side by side, and there was a broadening of the neural tube opposite the division of the notochord.

Professor FAWCETT said that a kinking of the notochord, comparable with that which occurs near the pituitary fossa, sometimes gives the appearance in certain sections of a division of the notochord which, however, does not really exist.

Professor T. B. JOHNSTON also communicated "A note on the development of the septum secundum of Born." Having recently found that the existence of the septum secundum as a distinct entity was seriously questioned in some quarters, he had been interested to discover the reasons for this scepticism. The structure which Tandler (Keibel and Mall's *Manual of Human Embryology*) identified as the septum secundum in the heart of a 9 mm. human embryo was regarded by Morrill (*Amer. J. Anat.* 1916) as one of two or three inconstant trabeculae which may be found in the roof and in the dorsal wall of the right atrium during the sixth and seventh weeks. The inconstancy of these trabeculae had been confirmed and probably accounted for the scepticism referred to. Sections of the heart of a 23 mm. human embryo were shown in which the septum secundum was easily identified as a substantial ridge on the dorsal wall of the right atrium. At this stage, the left venous valve is attached to the right side of the free border of the septum secundum and the dorsal attachment of the septum primum is situated on the left surface of the same structure; whereas, prior to the appearance of the septum secundum, both are attached to the dorsal wall of the right atrium.

The alteration in these attachments was explained by reference to the structure of the septum secundum, which was shown to be formed by an inflexion of the musculature of the atrial wall. Emphasis was laid on the presence in this embryo of a strongly developed septum secundum, while the septum spurium and the left venous valve were both present and intact throughout their whole extent. Attention was drawn to the fact that between the stages of 8 mm. and 23 mm. the left venous valve and the septum primum show very little modification in structure and appearance. From these observations it was concluded that, while there were still grounds for uncertainty with regard to its earliest stages, the septum secundum was a distinct embryological entity, and it was suggested that the process of inflexion of the muscular wall commenced in the region of the dorsal attachment of the left venous valve and subsequently spread so far leftwards as to involve the dorsal attachment of the septum primum.

Professor FRAZER said that the septum secundum was not present in

younger human embryos, e.g. the 11 mm. stage, the fold or folds to the right of the septum primum being the septum spurium, or "venous valves."

Professor FAWCETT remarked that there was a great range of variation in different hearts, and at different ages. He had one specimen in which no venous valve was present.

Mr T. NICOL communicated a paper on the "Uterus of Cavia after intra vitam staining with methylene blue." This will be submitted for publication in the *Journal of Anatomy*.

Mr A. J. E. CAVE demonstrated two abnormalities, descriptions of which are given in the following abstracts:

(*a*) *Ossification of the Hyoid Apparatus.* In lower forms the mesodermal tissue of the hyoid arch gives rise to a more complex series of permanent osseous structures than is met with in Man, but occasionally the human hyoid apparatus may manifest unusual elaboration by the substitution of true bony elements for fibrous tissue tracts of equivalent morphological value. In such instances the main divergence from the normal is brought about by the development, as a distinct epihyal element of that portion of the second arch cartilage which normally undergoes regression and becomes the stylohyoid ligament; further, as in the present case, the styloid process of descriptive anatomy may exhibit clear evidence of its compound nature.

The main interest in these uncommon variations is chiefly morphological as indeed is the case when elsewhere in the skeleton (e.g. suprascapular ligament, epicondylar spur or foramen, bony arch over vertebral artery) ligamentous structures are replaced by osseous tissue. Rarity, too, lends an added interest. Le Double (*Traité des Variations des Os du Crâne de l'Homme*, 1903, p. 348) encountered but one personal case, and was able to collect but nineteen others from the literature on the subject. Doubtless, however, our anatomical museums contain additional undescribed examples.

The specimen exhibited is from an adult male whose cranium presents no other unusual feature. Bilaterally the styloid process (about 3 cm. long) presents half-way down a nodosity suggesting the synostosis of two originally separate elements—an upper (tympanohyal) and a lower (stylohyal). Its inferior extremity is faceted for articulation with the subjacent epihyal, a styliform bony element, 42 mm. in length, which itself, replacing the stylohyoid ligament, articulates with the superior extremity of the small cornu (ceratohyal). Both ends of the epihyal bone, but especially the upper, bear the imprint of capsular attachments, and the same is true of the lower end of the styloid process, diarthrodial joints being necessitated by the movements of deglutition.

The body and cornua of the hyoid are well formed and normal, save that the tip of the left greater cornu is recurved inferiorly, the cartilago triticea being ossified in continuity therewith.

Professor FAWCETT commented on the great length of the tympanohyal.

Mr HARRIS mentioned a similar case of ossification of the whole hyoid apparatus in which the bone had been fractured by an osteopath.

(*b*) *Anomalous M. supinator longus.* The M. supinator longus is a very constant member of the radial group of forearm muscles, in appearance and attachments rarely departing from the standard description, and usually manifesting only those differences in degree of development which are em-

braced within the limits of normality. Its recorded variations may be briefly summarised as follows:

(1) *At its origin* the muscle is often blended with the brachialis anticus, and when its attachment ascends high upon the humeral shaft some continuity with the fibres of the deltoid is not infrequent. Two heads of origin have been reported by Testut and Macalister (*vide* Le Double, *Traité des Variations du Système Musculaire de l'Homme*, 1897, 2, p. 110).

(2) *The insertion* into the radius may ascend anywhere above the customary styloid level, and may be into the tuberosity, anterior oblique line, middle of shaft or outer border thereof at the level of the upper border of pronator quadratus; *per contra*, the insertion may descend to the carpus (scaphoid or trapezium) or metacarpus (rarely—and then usually into the base of the third metacarpal). Splitting of the tendon accounts for an occasional additional insertion into fascia or into a neighbouring extensor tendon.

(3) *Duplicity* has been noted in a few instances, the supernumerary member constituting the M. brachio-radialis brevis of Gruber or the M. supinator longus accessorius of Lauth.

(4) *Division of the muscle* most commonly affects the tendon providing the secondary insertions just mentioned, but more rarely a second muscular belly may be present blending with the biceps brachii or finding attachment "to the radius in the neighbourhood of the tuberosity or even to the ulna" (T. H. Bryce in *Quain's Anatomy*, 11th ed., 1923, IV (ii), p. 138). This ulnar insertion is seemingly the rarest form of attachment of any portion of the long supinator, for Le Double (*op. cit., supra*) quotes no single personal example nor any such case from his exhaustive review of the literature up to 1897. More interesting therefore is the present case, from an adult male subject.

The fibres of the left supinator longus intermingled with those of the deltoid and of the brachialis anticus, otherwise the muscle was typical. On the right side, the muscle's high origin exhibited marked continuity with the lowermost deltoid fibres, and received in addition a substantial accession of fibres from the triceps' outer head: there was no continuity with the brachialis. The muscle so formed divided just above the elbow into two bellies—the one having the normal disposition and inferior tendinous styloid insertion, the other and smaller passed medially to become a short flat tendon, which, passing deep to the brachial artery and the round pronator, gained insertion into the coronoid process. This additional belly and its tendon were throughout quite independent of the biceps and brachialis. The branch of the musculo-spiral to the main belly was found to provide a stout twig to the additional belly; but despite a careful search no branch from the same nerve to the outer portion of the brachialis could be discovered.

The innervation suggests that the extra supinator belly here present represents those lateral fibres of the brachialis normally supplied by the musculospiral (and here markedly differentiated from the main muscle mass) which are morphologically the equivalent of the outer head of the brachialis muscle in lower forms, and which belong to the extensor sheet. Support is given to this notion by the presence of the deltoid and triceps contributions.

Professor Barclay-Smith raised the question whether the variation should not be regarded as one involving that part of the brachialis anticus muscle which is supplied by the musculospiral nerve, rather than an anomaly of the supinator longus muscle itself.

Professor Le Gros Clark exhibited Marchi preparations showing the terminations of the optic tracts in the rat. Orr's modification of the Marchi technique (*J. Path.*, v, 6, 1900) was employed and found to give satisfactory results with paraffin sections. Very few optic fibres were found to remain uncrossed in the rat. The anterior accessory optic tract was clearly demonstrated, but could only be traced as far as the ventral surface of the pes pedunculi. No degenerated fibres could be seen penetrating the pes to reach the subthalamic nucleus as described by Loepp and others. The posterior accessory optic tract was also quite evident, and its fibres could be traced beyond the limits usually accorded to the nucleus opticus tegmenti into the medial extremity of the substantia nigra and to the tegmental area dorsal to this and lateral to the position of the red nucleus, reaching thus in the direction of the nucleus tegmenti lateralis. The dorsal and ventral nuclei of the lateral geniculate body were abundantly filled with degenerated fibres. Many of these pass through the ventral into the dorsal nucleus, and, again, through the dorsal nucleus into the pars posterior of the lateral nucleus (pulvinar). The sections indicate the practical certainty that the degenerated fibres seen in the pulvinar do not terminate there but pass through it entirely to reach the mid-brain. No degenerated fibres were found in the pretectal nucleus (which in the rat is relatively large). It seems, therefore, that the optic tract fibres that have been seen entering this nucleus in normal material are not retinal fibres, but probably fibres relayed on from the lateral geniculate body. A few degenerated fibres were found in the lateral part of the capsule of the pretectal nucleus, turning down between the pulvinar and this nucleus. There is in this situation a small and ill-defined group of cells which can be seen in sections stained with methylene blue and which appears to represent the large-celled nucleus of the optic tract described by the author in other Mammals. It is probable, also, that this group represents at least a part of Lewandowsky's nucleus paragenicularis in which Loepp found optic fibres terminating in the rabbit. No evidence was found of myelinated fibres of the optic tract reaching as far as the oculomotor nucleus as is stated to be the case by Tilney and Casamajor in the kitten.

Dr G. W. Nicholson gave a demonstration illustrated by lantern slides on a "Metanephros in a Teratoma."

Dr P. N. B. Odgers described a persistent circum aortic venous ring (renal collar), an account of which will be submitted for publication in the *Journal of Anatomy*, and a rare case of diaphragmatic hernia of which the following is an abstract:

The specimen came from the body of a woman, aged 65. The hernia had invaginated the diaphragmatic pleura and lay in the right pleural sac behind the right border of the sternum and the lower right costal cartilages, being moulded on the one side by the pericardium and on the other by the mediastinal surface of the right lung. The hernial sac, which was empty of contents, was divided by a complete septum into two loculi, the right of which was 2 inches, while the left was $1\frac{1}{2}$ inches in depth. A great deal of subserous fat separated the peritoneal sac from its pleural envelope. There was no abnormality in the attachment of the diaphragm. There was a well-marked muscular slip both from the right extremity of the bifid xiphoid cartilage and from the seventh right costal cartilage.

If traumatic cases are rigidly excluded, there are only twenty-three instances of hernia through this foramen recorded in the literature on the subject. Of these thirteen were found on the right side, five on the left, while five were bilateral. The only other case exactly like that recorded here was published by Lubosch (*Anat. Anzeiger*, 1918, LI, 249). Here the falciform ligament formed the septum dividing the sac into right and left loculi and the author thought that the hernia had a congenital basis in an irregular separation of the liver from the septum transversum.

Mr T. T. STAMM, introduced by Professor T. B. JOHNSTON, read a paper on "The constitution of the ligamentum cruciatum." This will be submitted for publication in the *Journal of Anatomy*.

Professor JOHNSTON alluded to the condition of the anterior annular ligament in the chimpanzee, and to the rediscovery by Professor BARCLAY-SMITH of the *ligamentum fundiforme*, originally described by Retzius.

Professor BARCLAY-SMITH drew attention to the relationship of the ligamentum fundiforme to the cavum tarsi, which is almost filled by this fundiform ligament, the interosseous ligament between the astragalus and os calcis being a comparatively weak structure.

Sir ARTHUR KEITH regarded the condition of the ligament in the human foot as evidence of Man having gone through a prehensile stage of existence.

Mr C. R. E. FREEZER, introduced by Professor T. B. JOHNSTON, exhibited two specimens illustrating arrested development.

The first, a median sagittal section of a male pelvis, showed a recto-prostatic pouch of peritoneum reaching down to the level of the last piece of the sacrum. The recto-prostatic septum was absent. The condition, therefore, represented the persistence of the early foetal arrangement.

The second was a very small microcephalic brain, weighing 39 gm., which was removed from an infant who survived 12 days.

The cavity of the diencephalon had been obliterated after the outgrowth of the optic vesicles and the hypophysis, and before the evagination of lateral ventricles from the fore-brain vesicle. The telencephalon was represented by a solid cortical operculum which had grown backwards over the diencephalon, without any attempt at bilateral symmetry, to stop short above the corpora quadrigemina. On its inferior aspect anteriorly there was a single large median olfactory bulb.

The mesencephalon and rhombencephalon presented normal foetal characteristics in those parts dependent for their substance on centripetal fibres, but were deficient in those formed from centrifugal fibres.

A detailed account of the anatomy of this specimen together with a number of physiological observations made during life will appear in the *Guy's Hospital Reports*, 1931.

Mr HARRIS remarked that anencephalic foetuses may remain alive for a period of about 3 hours. They die because they are unable to maintain a normal temperature. The obliteration of the third ventricle might be due to a concentration of commissural fibres in the massa intermedia. He enquired whether or no the weight of the suprarenals had been recorded.

Mr FREEZER in reply stated that the longest recorded case of survival of an

anencephalic foetus was 3 years. The infant, which was unable to regulate its temperature, was killed by being immersed in a too hot bath. The suprarenal glands in the case described were well formed.

MAY, 1931

THE Summer Meeting of the Society was held at the Queen's University, Belfast, on Friday and Saturday, 22 and 23 May, 1931. The President, Professor T. H. Bryce, in the Chair.

Professor E. T. R. EVATT communicated a paper on the "Lymphatic system and vitreous body of the eye," which will be published in the *Journal of Anatomy*.

The PRESIDENT enquired if Professor EVATT, during his investigations, had noticed any signs of protoplasmic threads of ectodermic origin between the lens and the optic cup. Professor EVATT replied that he had not observed such threads. Dr DAVIES suggested that if Professor EVATT's view regarding the hyaloid membrane were correct, the space containing the cerebrospinal fluid should communicate with the vitreous. Professor EVATT did not agree with this suggestion.

Dr E. P. STIBBE showed a specimen of Cyclopea in a newly-born child, and demonstrated the case with lantern slides. The special features of the case were:

(1) The entire absence of any proboscis. (2) Complete fusion of the optic diverticula to form a single median eye with no evidence of reduplication of the cornea, and with a large single median optic nerve and optic foramen. (3) Absence of any naked-eye evidence of a cerebrum. (4) Persistence of an embryonic condition of the cranial blood sinuses. (5) Congenital morbus cordis—namely, complete stenosis of the pulmonary artery, patent interventricular septum and ductus arteriosus. The child lived two days.

A histological study of the brain is being carried out, and a full report with illustrations will be submitted for publication in the *Journal of Anatomy*.

Professor WOOLLARD enquired whether or no situs inversus was present. Dr STIBBE replied that the viscera were normal in position with the exception of the aorta which was disposed on the right side.

Mr H. J. KIRKPATRICK read a paper on the "Radiological investigation of the alimentary tract."

Professor WATERSTON drew attention to the rapid movements seen in the colon and commented upon their physiological importance.

Dr H. A. HARRIS said that the position of the viscera was determined in the living subject by the necessity of maintaining the patency of the hollow ducts during activity, and referred to the work of Mills on bodily habitus.

Professor G. ELLIOT-SMITH exhibited a series of casts and photographs of the Peking Skull, a full account of which is published in the Henderson Trust Lectures, No. XI: *The Significance of the Peking Man*. University of Edinburgh.

The PRESIDENT congratulated Professor ELLIOT-SMITH on his admirable exposition of the importance of the skull, and the inferences which he had made therefrom.

Dr W. E. HARPER, collaborating with Professor D. R. DOW, read a paper on "The vascularity of the cardiac valves."

Professor WALMSLEY suggested that before accepting any vascularity of the valve as being normal, endocarditis must be absolutely excluded, as minute subendocardial nodules were frequently present, although any macroscopic evidence of their existence was absent.

Dr J. S. CAMPBELL was of the opinion that the valves were probably avascular in the normal heart.

Dr F. DAVIES said that it was remarkable that ventricular muscle should have entirely disappeared from the tricuspid valve whereas auricular muscle was present, in view of the fact that in the bird's heart the right auriculo-ventricular muscular valve consisted mainly of ventricular muscle.

Dr J. S. CAMPBELL communicated a paper on "The blood supply of the cardiac septum."

Professor WALMSLEY emphasised the importance of the variability of the blood supply to the neuro-muscular tissue.

Professor DOW and Professor WATERSTON also took part in the discussion.

Dr DAVIES hoped that, in view of the work of Gross, Dr CAMPBELL would study how far age changes affect the degree of septal anastomosis.

Mr J. S. LOUGHRIDGE and Mr J. S. BLACKSTOCK communicated a paper on the "Efferent paths to blood vessels," of which the following is a summary:

Methods have been employed to investigate the structural and functional changes resulting from an interruption of: (1) the pre-ganglionic sympathetic pathway, (2) the post-ganglionic sympathetic pathway, (3) the perivascular network.

Structural changes have been investigated by Nevin in cases of unilateral lumbar sympathectomy in the dog. In all cases the sympathetic cord below the section has been examined for changes in the ganglia, the internodes and the grey rami, and in the main limb nerves, motor and sensory. The only definite structural change following a pre-ganglionic lesion is in the ganglion immediately below the section. Here the pericellular network, as shown in silver pyridene preparations, has disappeared.

After a post-ganglionic sympathectomy changes occur in the grey rami and peripheral nerves. In the former there is a marked decrease in the medullated fibres in the operated compared with the normal, e.g. in the grey ramus of the 7th lumbar ganglion there are two white fibres compared with fifty-six on the normal side. These medullated fibres are post-ganglionic, as all pre-ganglionic fibres have undergone degeneration. In the peripheral nerves those amyelinated fibres which are scattered among the myelinated fibres undergo degeneration. Certain amyelinated fibres remain in peripheral nerves after this operation and may be of dorsal root origin. They are found mainly in association with little bundles of small myelinated fibres. No changes were found in the voluntary muscles on the operated side.

The disturbances produced in the vascular supply of the skin by the above-mentioned operations have been investigated by the determination of the skin temperature by thermocouples. Temperature differences in the normal and operated sides are readily demonstrated in the resting animal and after the circulation in the part has been disturbed by gravity, exercise, heat and cold,

etc. On the day following a lumbar sympathectomy the temperature difference may be as much as 10° C. (the actual figures being 20·7 and 30·3° C.). This difference diminishes in time in the resting state but can always be brought out again by any condition producing vaso-constriction of the normal limb. No loss of vaso-motor control has been found to follow periarterial sympathectomy.

Attempts have been made recently to detect action currents in cutaneous nerves before and after sympathectomy, and there is some evidence to show that there is a difference corresponding to the structural and functional changes described above.

Dr R. H. HUNTER read a paper on "Extrauterine pregnancy in a cat," which will be submitted for publication in the *Journal of Anatomy*.

The PRESIDENT said the case was one of unusual interest, and agreed with Professor PATTEN's interpretation of the placental site.

Dr D. STEWART communicated a paper for Miss EUGENIE R. A. COOPER on the "Development of the pineal gland and its relation to pineal cysts." The paper will be submitted for publication in the *Journal of Anatomy*.

Professor T. WALMSLEY read a paper on the "Vertical axes of the femur," which will be submitted for publication in the *Journal of Anatomy*.

Professor ELLIOT-SMITH agreed with Professor WALMSLEY in considering that the chimpanzee represented a retrograde type, and suggested further that Neanderthal Man was also retrograde in type. He also suggested that *Dryopithecus* was the only primate which was in the direct line of human descent. Professors EVATT and WATERSTON and Mr RALPH THOMPSON also took part in the discussion.

Dr H. A. HARRIS communicated papers on (1) "Methods of tracing age changes in the skull," and (2) "The rôle of the epiphyses in relation to growth."

The PRESIDENT complimented Dr HARRIS on the presentation of these facts in a manner unfamiliar to many members of the Society. In the discussion which followed Professor BLAIR stated that he had seen blood vessels passing from the diaphysis to the epiphysis, through the epiphyseal line.

Dr HARRIS agreed that this might occur, and stated that the terms "atavistic," "pressure" and "traction" as applied to epiphyses probably did not deserve the importance hitherto assigned to them.

Professor C. M. WEST read a paper on the "Post-glenoid tubercle," which will be submitted for publication in the *Journal of Anatomy*.

Mr H. GOODING and Mr D. STEWART presented a paper on the "Fixation and decalcification of bone." The communication contained an account of an investigation into the actions of various combinations of fixatives and decalcifying agents upon histological structures of bone.

The fixatives chosen were, 10 per cent. formol, Zenker, Bouin's, mercuric chloride, and 90 per cent. alcohol. The decalcifying solutions used were, 30 per cent. formic acid in 5 per cent. formol, 5 per cent. nitric acid in 5 per cent. formol, 10 per cent. hydrochloric acid in 5 per cent. formol, 10 per cent. hydrochloric acid in 90 per cent. alcohol, 30 per cent. formic acid, and 5 per cent. nitric acid.

The femora from freshly killed rabbits were sawn into small pieces and placed in the different fixatives for 48 hours. The specimens which had been fixed in Zenker's and mercuric chloride were washed in water for 24 hours and the preparations were then immersed in the decalcifying agents. These were changed daily until decalcification was completed, which was tested by pricking with a needle. The blocks of bone were cut on a freezing microtome and the sections were at once stained with haemalum and eosin, and mounted in glycerine jelly.

Blocks were prepared in each fixative and in all the different decalcifying agents, consequently a complete series was obtained of all the possible combinations of fixatives and decalcifying agents used in the investigation.

The stained sections were examined microscopically and their degree of merit estimated by considering (1) the amount of shrinkage and quality of staining of the bone cells, (2) the amount of shrinkage and quality of staining of the contents of the Haversian canals, (3) the amount of shrinkage of the lacunae, (4) the quality of the stain in the ground substance.

Table I. *Fixative:* 90 °/₀ *alcohol*

Decalcifying agent	Bone cells		Haversian canal		Shrinkage of lacunae	Stain of ground substance	Total
	Shrinkage	Stain	Shrinkage	Stain			
30% formic in 5% formol	3	1	2	2	3	½	11½
5% nitric in 5% formol	1	1	1	½	2	1	6½
10% hydrochloric in 5% formol	½	½	1	1	1	2	6
10% hydrochloric in 90% alcohol	3	2	1	–	3	1	10
30% formic	½	½	½	½	2	1	5
5% nitric	2	½	–	–	1	1	4½
Total	10	5½	5½	4	12	6½	43½

Table I shows the type of result obtained from the combination of one of the fixatives with the different decalcifying fluids, and Table II the converse results with one of the decalcifying fluids and the fixatives.

Table II. *Decalcifying agent:* 30 °/₀ *formic acid in* 5 °/₀ *formol*

Fixative	Bone cells		Haversian canal		Shrinkage of lacunae	Stain of ground substance	Total
	Shrinkage	Stain	Shrinkage	Stain			
10% formol	½	1	1	½	½	1	4½
Zenker	2	½	–	–	1	2	5½
Mercuric chloride	2	2	1	½	3	3	11½
Bouin's	1	2	1	2	½	1	7½
90% alcohol	3	1	2	2	3	½	11½
Total	8½	6½	5	5	8	7½	40½

Marks were allotted as follows: bad, 0; poor, ½; fair, 1; good, 2; very good, 3. It was realised that errors were likely to arise from the personal prejudices of the examiner. This was avoided by one of the investigators carrying out the whole of the preliminary work, while the judging was done by the other, who did not know how the sections he was examining had been prepared.

Tables similar to I and II were made for each of the reagents, and summaries of the total marks obtained by them are shown in Tables III and IV.

Table III. *Fixatives*

	Bone cells		Haversian canal		Shrinkage of lacunae	Stain of ground substance	Total
	Shrinkage	Stain	Shrinkage	Stain			
90% alcohol	10	5½	5½	4	13	6½	44½
Mercury	7½	7	5	3½	7	10	40
Bouin's	6	7	6	8	6½	6½	40
10% formol	3	1½	6	4½	8½	7	30½
Zenker	3½	1	3½	3½	3½	5½	20½

Table IV. *Decalcifying agents*

30% formic in 5% formol	8½	6½	5	5	8	7½	40½
10% hydrochloric in 90% alcohol	7	6	4½	7	5½	10	40
5% nitric	9	2	6	2	6½	3½	29
5% nitric in 5% formol	2½	3½	3½	2½	8½	4	24½
30% formic	2	2½	3½	4	6	4	22
10% hydrochloric in 5% formol	1	1½	3½	3	3	6	18

From these it will be seen that of the fixatives, 90 per cent. alcohol, mercuric chloride, and Bouin's gave distinctly better results than 10 per cent. formol or Zenker; while 30 per cent. formic acid in 5 per cent. formol and 10 per cent. hydrochloric in 90 per cent. alcohol were superior to the other decalcifying fluids.

Table V

Fixative	30% formic in 5% formol	10% hydrochloric in 90% alcohol
Mercury	11½	9½
Bouin's	7½	11
90% alcohol	11½	10

Table V shows the total marks obtained by sections treated with combinations of the successful fluids mentioned above.

To confirm these results, the combinations shown in Table V were repeated and the opportunity was taken of adding 10 per cent. aqueous hydrochloric acid to the decalcifying fluids. The results of these experiments are shown in Tables VI and VII.

It will be seen from Table VI that Bouin now proved to be definitely inferior to mercuric chloride or 90 per cent. alcohol as fixatives, while 30 per cent. formic acid in 5 per cent. formol is superior to the other decalcifying agents. These results therefore show that fixation with either 90 per cent. alcohol or mercuric chloride followed by decalcification in 30 per cent. formic acid in 5 per cent. formol will give the most satisfactory histological preparations of osseous tissues.

It was stated at the beginning of this communication that glycerine jelly was used as the mounting medium for our preparations. This was chosen

Table VI. *Fixative: Mercuric chloride*

Decalcifying agent	Bone cells: Shrinkage	Bone cells: Stain	Haversian canal: Shrinkage	Haversian canal: Stain	Shrinkage of lacunae	Stain of ground substance	Total
30% formic in 5% formol	2	3	3	–	1	3	12
10% hydrochloric in 90% alcohol	½	–	2	–	2	2	6½
10% hydrochloric in water	3	½	1	–	3	2	9½
Total	5½	3½	6	–	6	7	28
Fixative: Bouin's							
30% formic in 5% formol	–	–	2	½	1	3	6½
10% hydrochloric in 90% alcohol	–	–	½	1	½	2	4
10% hydrochloric in water	3	½	–	½	–	2	6
Total	3	½	2½	2	1½	7	16½
Fixative: 90% alcohol							
30% formic in 5% formol	3	3	3	3	2	3	17
10% hydrochloric in 90% alcohol	1	1	½	–	2	2	6½
10% hydrochloric in water	3	½	2	–	1	2	8½
Total	7	4½	5½	3	5	7	32

Table VII. *Decalcifying agent: 30% formic acid in 5% formol*

Fixative	Bone cells: Shrinkage	Bone cells: Stain	Haversian canal: Shrinkage	Haversian canal: Stain	Shrinkage of lacunae	Stain of ground substance	Total
Mercury	2	3	3	–	1	3	12
Bouin's	–	–	2	½	1	3	6½
90% alcohol	3	3	3	3	2	3	17
Total	5	6	8	3½	4	9	35½
Decalcifying agent: 10% HCl in 90% alcohol							
Mercury	½	–	2	–	2	2	6½
Bouin's	–	–	½	1	½	2	4
90% alcohol	1	1	½	–	2	2	6½
Total	1½	1	3	1	4½	6	17
Decalcifying agent: 10% HCl in water							
Mercury	3	½	1	–	3	2	9½
Bouin's	3	½	–	½	–	2	6
90% alcohol	3	½	2	–	1	2	8½
Total	9	1½	3	½	4	6	24

because it was found, in the earlier stages of the investigation, that the necessary dehydration required for mounting in Canada balsam of frozen sections caused marked shrinkage of all the tissues, especially of the bone cells. Embedding in paraffin was discarded for the same reason. The employment of xylol, butyl alcohol, cedar wood oil, or chloroform as clearing agents appeared to make little difference to this shrinkage.

Only one objection was found to the use of glycerine jelly and this is due to the fact that eosin tends to diffuse into the jelly, which interferes with the sharpness of the preparation and mars the permanency of the specimen. Various other stains were tested but did not prove to be more satisfactory.

During the discussion Dr H. A. HARRIS had suggested the use of mercurochrome instead of eosin. We have since tried this stain, and although there is still a slight amount of diffusion, it is vastly superior to eosin. We would like to take this opportunity of thanking Dr HARRIS for his suggestion.

The President, Professor T. H. BRYCE, demonstrated a series of ancient Scottish femora and tibiae.

The bones exhibited came from certain graves in Caithness dated about the tenth century, and from an underground dwelling in Orkney of unknown date. They were described in a paper published by the Society of Antiquaries of Scotland[1].

In discussing Professor BRYCE's paper Professor WALMSLEY compared the torsion of these femora to that normally found in the foetal humerus, and thought that the femoral torsion should be correlated with the position of extension rather than flexion, since the thighs in quadrupeds are in the position of flexion and in them there is no trace of torsion. Torsion is not present in Neanderthal Man, but is present in *Pithecanthropus*. Professor WOOLLARD, Dr HARRIS and Dr INKSTER discussed the squatting attitude amongst Scottish miners, and the general opinion was that this attitude was not of the same nature as that adopted by these early people. Dr INKSTER suggested examining the talus as giving a possible clue to the attitude which was adopted by them. Dr DAVIES stated that the recurved form of the upper end of the tibia in the specimens exhibited was a normal feature in the child at birth, and probably was to be correlated with the position of the foetus *in utero*.

Dr M. A. MACCONAILL read a paper on "The function of intra-articular fibrocartilages" of which the following is a summary. It was shown by reference to the theory of lubrication, that intra-articular cartilages are to be related

[1] *Proc. S. A. S.* vol. LXI, p. 301. The interest of the collection was the evidence the bones provided of adaptive variations. The tibiae besides showing a varying degree of retroversion of the head—convexity of the lateral condylar surface and so-called "squatting facets"—had a very high average angle of torsion. The femora also exhibited a high angle of torsion—due to an outward twist in the upper third of the bone. The degree of this varied but in many specimens was so pronounced that the normal anterior surface was directed lateralwards, and the head and neck forwards to an abnormal extent. These features suggested some adaptation to the mode of life of these early people in the low-roofed underground dwellings such as that from which the second series of bones was recovered. The changes in the tibiae corresponded to those long ago described in living races who habitually adopted the squatting posture—but the high degree of torsion both of the tibiae and femora was less easily explained. No such large series of ancient bones from the Scottish area exhibiting their features has hitherto been described.

primarily to the synovial fluid rather than to the articular surfaces of the bones. They so act as to bring about the formation of wedge-shaped films of synovia in relation to the weight-transmitting parts of joints in movement. These wedges are convergent in the direction of motion, and are essential for weight transmission. Such cartilages are to be found in joints in which thrusts are likely to bring about premature approximation of the surfaces. Preparations were described of the knee and inferior radio-ulnar joints, which demonstrate their action. These also show that the cartilages are congruent with articular surfaces only in the "weight-carrying" position of the joints (position of stability).

Dr A. J. E. Cave presented a paper on the "Definition of the cervical pleurapophyses."

Professor D. M. Blair read a paper on "Congenital absence of the tibia." The paper will be submitted for publication in the *Journal of Anatomy*.

Mr Ralph Thompson described a case of "Congenital stricture of the urethra." The President said the stricture was not so far back that it could not be explained on the assumption that a failure had occurred in the fusion of the ectodermal and entodermal parts.

Professor G. Elliot-Smith read a paper on "Structural revolution in the central nervous system." The President said that the meetings of the Society had for the last 35 years been illuminated by the brilliant expositions of Professor Elliot-Smith on the evolution of the central nervous system. The present address was no exception to the rule. Professor Woollard enquired if the olive was not the instrument of the thalamus and the pons that of the cerebrum? Professor Elliot-Smith in replying said he thought that the olive was more probably the instrument of the corpus striatum and the tectum.

Professor H. Woollard communicated a paper on "The sympathetic and the brachial plexus." Reference was made to the composition of the intermediate grey matter in the lower cervical region and the possibility that sympathetic axons might start from cells other than those of the lateral horn.

The size of the fibres in the ventral roots was not a feature by means of which the presence or absence of sympathetic axons could be determined, since it is known that some somatic motor fibres do not exceed 2μ in diameter.

The rami joining the roots of the brachial plexus are, however, almost completely non-medullated. This holds good for the fibres composing the ramus vertebralis. From dissection and histological analysis it was concluded that there was no good reason for believing that in Man pre-ganglionic fibres reached the cords of the brachial plexus other than by way of the upper thoracic ventral roots. Post-ganglionic fibres start from the 1st thoracic ganglion, and the inferior and middle cervical ganglia. There is no evidence of Winkler's suggestion that they may ascend through the roots of the spinal accessory and be transferred from this nerve to the cervical sympathetic chain. The only possible variation is that of Langley and Harmer, viz. the variation associated with pre-fixed, middle and post-fixed plexuses. Judging from the number of rami and preliminary counts of the axons contained in these it is

inferred that the caudal roots of the plexus receive the greater number of post-ganglionic fibres.

The post-ganglionic fibres have a cutaneous distribution corresponding to the nerves which they accompany. This was proved by blocking the nerves with 4 per cent. novocaine and 1 in 60,000 adrenalin which paralysed the vasoconstrictors. The area of vasodilatation corresponded exactly with the area of distribution of such nerves as the ulnar, median, etc. The vasomotor distribution could be observed by noting the distribution of the flush and by observing the rise of temperature by means of a thermopile. The flush and rise of temperature were greatest over the digits and the palm of the hand and the sole of the foot but were limited to the anatomical area of the particular nerve which was injected.

Professor ELLIOT-SMITH expressed pleasure at the graceful tribute which Professor WOOLLARD had paid to the memory of Professor John I. Hunter and Dr N. D. Royle. The paper was commented on by Professors BLAIR and WATERSTON, and Drs MACCONAILL, STEWART, THOMPSON, HARRIS, DUNLOP, and BEATTIE. Mr RALPH THOMPSON was sceptical of the results obtained by sympathectomy for the relief of spastic conditions of the extremities. Professor WOOLLARD pointed out that the operations were performed for the relief of arterial spasm and not for spastic paralysis. The surgical results at St Bartholomew's Hospital were parallel with those obtained by other workers.

Professor J. BEATTIE read a paper on "The secretory mechanism of the lachrymal gland." This paper was a summary of experimental work carried out by Professor BEATTIE and Mr R. MACDONALD. Evidence was produced that the parasympathetic nerves do not innervate the portions of the gland which obtain a supply from the true sympathetic system. Experimental evidence for the existence of myo-epithelial tissue within the gland and of smooth muscle within the short ducts was given, but it was pointed out that until histological work had been completed the results given were purely tentative.

Professor WOOLLARD pointed out that morphological conclusions should not be drawn from pharmacological evidence alone. Professor WATERSTON and Dr DUNLOP also took part in the discussion. Professor BEATTIE agreed with Professor WOOLLARD's contention.

Professor BEATTIE made a further communication on the "Hypothalamic pupillo-dilator centre."

Professor I. MACLAREN THOMPSON described certain "Experimental work on cutaneous innervation" carried out in the Anatomical Laboratory of the University of California in collaboration with Messrs Verne, T. Inman and Bernard Brownfield.

It was found that unipolar stimulation of a cutaneous or of a mixed nerve trunk (through the skin) in a conscious human being by means of an alternating current of appropriate frequency and strength rendered the cutaneous area supplied through that nerve insensible to light touch.

By this technique all the main nerve areas of the forearm and hand were outlined and measured in sixty-five limbs of male medical students.

It was shown how the results may be used to estimate the range of normal variation in the size of these areas in the young adult male population at large, particularly if count be taken of the influence of variation in limb size upon

that of the cutaneous nerve areas. The latter may be effected, in the case of each area, by the use of the standard deviation about the regression line of that area upon the total cutaneous area of the forearm and hand.

Dr R. D. LOCKHART made the following communications:

(1) "A rapid and simple histological method of making complete sections through the entire human brain." Actual sections were shown by the transmitted light of the epidiascope. By means of the microtome and method of Hamilton[1], slabs of brain 1½ inches thick may be readily frozen, and cut as easily as a joiner planes a piece of wood.

The real secret is the freezing fluid in which the tissue is soaked. This is composed of sugar, mucilage, and water, in certain proportions. The more delicate the tissue and the greater its liability to damage from ice crystals, the more syrup and mucilage are used, until a mixture which barely freezes is obtained.

The appearance of the microtome is not imposing in contrast with the ponderous size and meticulous refinement of modern machines, but a single trial will yield beautiful evidence in justification of Hamilton's enthusiastic delight.

As serial sections of the entire human brain may be cut within three weeks from receiving the specimen, the method is both simple and rapid.

(2) (In association with Dr GREIG ANDERSON.) "A case of lateral syndrome of the medulla." The patient, a man aged 60 years, felt a slight giddiness at dinner and was unable to swallow even a drop of fluid. Examined in hospital, he was found to lodge a barium bolus behind his cricoid, and a stomach tube could not be passed. This persistent inability to swallow fluids is the salient feature of the case. The patient also exhibited contracted right pupil, refusing to dilate on stimulation of the sympathetic in the neck. Retracted eyeball, with apparent drooping of the lid and narrowing of the canthus, that is, the sign group of Horner's Syndrome; loss of pain and temperature sensation up to the umbilicus on the left extremity and trunk; paralysis of the right palate and right superior constrictor, with the *mouvement de rideau*; abolition of the nausea reflex; and defective taste on the right side of the tongue.

In the light of the literature of twenty-three cases, and the conflicting views of thirty texts, the anatomical, physiological, and clinical features of the cases were discussed with especial reference to the neurological mechanism of swallowing.

(3) "The acrobat in radiogram." The communication was illustrated by lantern slides and will be submitted for publication in the *Journal of Anatomy*.

The following communications from Professor C. J. PATTEN were taken as read:

(1) An unusual muscular variation at the wrist. During the Winter Session, 1931, an accessory head of the abductor digiti quinti, associated with an anterior carpal slip arising in common with it, was found in the right wrist of an aged dissecting-room male subject. The muscle arises by a fleshy mass from the attachments of the outer side of the anterior annular ligament. From this proceeds a strong strap-shaped band, ¾ cm. The fibres are superficial to, and distinct from, the ligament, and are divisible into proximal parallel fibres and

[1] *Text Book of Pathology*. D. J. Hamilton, 1889, vol. I, p. 65 and pp. 58–59. Macmillan & Co., London.

distal converging fibres. The separation between the two sets begins adjacent to the pisiform bone. The proximal fibres pass to the pisiform and there obtain a fleshy insertion. They replace the superficial transverse ligament, and accordingly pass in front of the ulnar vessels and nerve. The distal fibres join the abductor minimi digiti on its outer side. The muscle is not divisible at its origin, and is supplied by a single branch of the deep division of the ulnar nerve.

The palmaris longus muscle is distinct from, and superficial to, the whole structure. The palmaris brevis is well developed, and is supplied by the usual branch from the superficial division of the ulnar nerve. No corresponding abnormality is present on the other side. The muscles of both upper limbs are well developed.

The variation clearly consists of two parts: one, the accessory head of the abductor digiti quinti, a variation already recorded; the other, the band of transverse fibres which replaces the superficial transverse ligament, and may be called a *musculus transversus carpi anterior*. Le Double makes no mention of such a slip, nor is it recorded in Quain. Doubtless, records of future similar cases will assist in determining its true morphology, which is at present quite obscure. I am much indebted to Dr MacConaill for his careful dissections.

(2) A case of "Absence of the corpus callosum." The brain is that of a female aged 55 years. She was admitted to the South Yorkshire Mental Hospital in 1907, and died after 6 months. She was affected with acute mania, and there were, in addition, some delusions regarding money. The cause of death as recorded was "Atrophy of the brain." The insanity was of only 8 months' standing. The brain is of fair size: 170 mm. fronto-occipital length, 140 mm. parietal breadth, and 100 mm. height, measuring from the vertex to a plane corresponding to the lower surfaces of the temporal lobes. It is highly convoluted, although the several gyri are somewhat small in size. The principal convolutions can easily be distinguished.

There is a total absence of the corpus callosum, nor is there any trace of the *anlagen* of such a structure. There is, however, a well-defined band of longitudinal white fibres in the position of the cingulum. This band passes (in each hemisphere) over the chorioid plexus of the lateral ventricle. The anterior commissure is large, and the mammillary bodies well developed. There is no massa intermedia between the thalami. The remaining parts about the third ventricle are normal, although the fornices are small and unconnected.

The cavities of the lateral ventricles are very large and smooth-walled. The eminences in their walls are easily recognisable, but are somewhat flattened. Each ventricle was sufficiently large to contain 70 c.c. of fluid (in the hardened brain), an amount equal to the total quantity of cerebrospinal fluid in the normal person. There is, then, a definite enlargement of the lateral ventricles in this case: that is, a sub-hydrocephalic condition. The medial wall of the ventricle is more than usually thin, no doubt an atrophy from pressure.

Apart from these rare anatomical conditions, the specimen is interesting from the psychological point of view. The insanity was of short duration, and the chief delusions recorded had to do with money. From this it may be argued that the patient had already acquired some knowledge of symbolic representation, and had been, therefore, at least moderately developed intellectually. This case, then, falls into the group in which absence of the corpus callosum is not incompatible with a high degree of functioning of the brain.

JUNE, 1931

AN Ordinary Meeting of the Society was held at King's College, London, on Friday, 19 June, 1931, Professor Mary Lucas Keene, Vice-President, in the Chair.

Dr JOHN BRANDER, introduced by Professor T. B. JOHNSTON, read a paper on the "Intraglandular cleft of the pituitary body, and its connections." The paper was illustrated by numerous lantern slides of microphotographs, and will be submitted for publication in the *Journal of Anatomy*. In the discussion which followed, Professor JOHNSTON congratulated Dr BRANDER on the completeness of his work, and the beautiful series of microphotographs which he had exhibited. Professor BEATTIE stated that with every increase in intracranial pressure colloid is expressed from the pituitary gland. Perforation of the floor of the pituitary fossa, and large blood spaces communicating with the veins issuing from the pituitary body are undoubtedly present in certain cases. Dr UNA FIELDING said that she had obtained no evidence of persistence of the intraglandular cleft in the adult. In some cases the floor of the pituitary fossa was absent.

Professor J. BEATTIE reported a case of "Cerebellar Agenesis." The anomaly was discovered in a male adult who had died aged 42 years. The history of the case was very incomplete, but there was no doubt that the condition had existed during the whole of life. The limbs alone were affected, both sides and both upper and lower extremities equally. The disability consisted of muscular weakness and ataxic movements. The patient was able to sit upright and to speak without difficulty.

The cerebellum consisted of two very small hemispheres and a vermis. The left hemisphere was about the size of a walnut and the right little larger than a pea. The vermis was reduced to about half the normal size. The concavity of the occipital bone was obliterated but otherwise the posterior fossa was normal. Microscopically, the vermis showed a structure which was not considered abnormal. The Purkinje cells of the hemispheres were very much reduced in number in all fields and those remaining were atrophic and showed signs of reduction of the dendritic processes. A complete study is being made of the brain stem and cortex.

Professor ELLIOT-SMITH emphasised the importance of accurately recording all cases of cerebellar defect, and enquired whether there were any changes in the cerebral cortex. Professor LE GROS CLARK enquired whether there was any disorder of the muscular tone, and whether Dr BEATTIE proposed to investigate the cortex of the whole cerebral area. Professor BEATTIE replied that there was a loss of muscular tone over the whole body. He did not think it was practicable to examine the whole area of the cerebral cortex!

Professor MACLAREN THOMPSON read a paper on the "Cavum septi pellucidi," which has been submitted for publication in the *Journal of Anatomy*. Professor ELLIOT-SMITH alluded to the work of Owen and Flower, who questioned the presence of an actual cleft in lower mammals, e.g. insectivores. Hochstetter has described it as a secondary condition in the human foetus. The condition described by Dart was extremely common in hydrocephalic

brains. Rudolf Virchow believed that a natural communication existed between the third ventricle and the fifth ventricle which afterwards became closed. The cleft can easily be demonstrated in Primates. It was situated in the paraterminal body. Professor Le Gros Clark corroborated the statements made with reference to the absence of a true cavum septi pellucidi in insectivores, although there was a slight recession of the cavity of the third ventricle into the septum. Professor Frazer alluded to the double nature of the paraterminal body and suggested that the two parts, which come in contact with each other during development, may afterwards draw apart.

Dr E. P. Stibbe for Dr F. Davies, Dr R. J. Gladstone and himself read a paper on the "Anatomy of the intercostal nerves." The communication was a result of dissections of adult and still-born subjects carried out at University College, King's College and London Hospital Medical College. The paper will be submitted for publication in the *Journal of Anatomy*. In discussing the distribution of the intercostal nerves to the rectus abdominis in Man, Dr F. Davies called attention to the experimental observations of Ross Harrison on the motor and sensory components of the nerves to the abdominal wall and their relations to the rectus muscle and its tendinous intersections in the frog. Professor G. Elliot-Smith congratulated the authors on the completeness and importance of their work, and stated that the method of distribution of the intercostal nerves to the rectus abdominis in Man described by the workers was very suggestive in view of the work of Ross Harrison. Mr A. Ralph Thompson also emphasised the importance of the distribution of the last dorsal nerve to the rectus and pyramidalis muscles in respect of the employment of these muscles for the surgical repair of the lower abdominal wall in cases of epispadius and ectopia vesicae.

Dr R. J. Gladstone read a paper on the "Development of the sternum," which will be submitted for publication in the *Journal of Anatomy*. He also showed on behalf of Dr J. Taliat a reconstruction model of the episternal region of a mouse embryo, and for Mr E. McClellan a model of the sternum of a rabbit embryo. The model of the mouse embryo represented an early stage in the development of the sternum in which the cartilaginous hemisternebrae had not reached the median plane, and were not yet completely united with the ventral ends of the ribs. The model of the rabbit embryo represented a later stage in which some of the cartilaginous hemisternebrae had united with each other in the median plane and in which they had also fused with the tips of the rib-cartilages. The demonstration was illustrated by lantern slides showing the early bilateral condition of the sternum and its relation to the shoulder girdle in extinct amphibia and reptiles of the Permian age (Broom, *Eosuchia Youngina*, and Piveteau, *Hovosaurus*, *Tangosaurus*). In these the sternum appears, in the fossils of the younger animals, to have originated as two oval plates of bone which are situated posterior to the similar coracoidal plates, and were probably laid down in cartilage. In the fossils of older specimens the two plates were so fused as to form a single median plate.

Dr M. A. MacConaill read a paper on "The mechanism of the radio-ulnar joints," of which the following is a summary. The curvatures of the several parts of the radio-ulnar joints are ellipses of constant form and equal value.

This ensures the formation of pressure films of synovia during movement. The surfaces are incongruent except in one position—the synarthrodial. The position of complete coäptation is at three-eighths of pronation. It is attained by the aid of a screw mechanism. This mechanism brings about a locking of the joints and converts the antebrachial skeleton into a "girder." The interosseous membrane occupies the neutral area of the girder, and takes no share in the transmission of strain. The significance of the synarthrodial position of diarthroses is discussed, and it is defined functionally to be the synergic position of a joint. By means of it separate components are grouped into single working units, which are further associated in the performance of "mass actions" by the individual.

Dr HARRIS congratulated Dr MACCONAILL on having brought these facts, which are known in the engineering world, to the attention of the Society.

Dr Y. H. AASAR read a paper on the "Prochordal plate in the rabbit," which will be submitted for publication in the *Journal of Anatomy*.

Dr ALWYN T. COMPTON described a case of Partial Situs Inversus. This condition was found in a woman aged 30 years, who was operated on for symptoms indicating the presence of gastric ulcer. The woman was the mother of two healthy children. In neither of these children was there any evidence of situs inversus being present. At the operation the stomach spleen and pancreas were seen to be reversed. The great omentum was absent. The duodenum, the rest of the small intestine and the large intestine were all suspended by a dorsal mesentery which was median and almost straight in position. The small and large intestine were abnormally short, probably less than two-thirds of their usual length.

The thoracic organs of the mother were found on X-ray examination to be normal. The elder child has an unusually horizontal stomach.

Professor D. M. BLAIR, Dr F. DAVIES and Dr E. W. MCCLELLAND communicated a paper on "Differential staining of thick sections of brain." The paper was read by Professor D. M. BLAIR, and will be submitted for publication in the *Journal of Anatomy*.

Specimens of brain coloured with various chemical substances were exhibited.

Professor D. M. BLAIR, Dr F. DAVIES and Dr E. W. MCCLELLAND communicated a paper (read by Professor D. M. BLAIR) on the "Preparation of 'dry' specimens by paraffin naphthalene impregnation." Owing to lack of time this paper was read in conjunction with that on the "Differential staining of brain sections."

This paper will also be submitted for publication in the *Journal of Anatomy*.

Professor F. KISS gave a demonstration on "The relationship between vagus and sympathetic in the Vertebrates."

The demonstration consisted of two parts: a microscopical and a comparative anatomical. The microscopical part was the analysis of the nerve fibres in the human vagus. This analysis was based upon a previous investigation of

Professor Kiss[1] in which he differentiated microscopically the following nerve fibres:

(*a*) the voluntary motor fibres of the cranial and spinal nerves are (according to previous authors) without exception heavily myelinated fibres;

(*b*) the sensory fibres of the cranial and spinal nerves are without exception thinly myelinated fibres;

(*c*) the pre-ganglionic fibres of the sympathetic are always thinly myelinated—whereas the post-ganglionic fibres of the sympathetic are always unmyelinated;

(*d*) the thinly myelinated fibres of the anterior spinal roots are all pre-ganglionic fibres; the variation in their number depends upon the size of the white ramus communicans, by which the spinal nerve is connected with the sympathetic trunk (their number is low in the cervical segments and high in the dorsal segments).

Professor Kiss cannot yet determine the nature of the large myelinated fibres of the posterior spinal roots and of the sensory cranial nerves. These are in a minority in these nerves, in which they have the same thick myelin sheath as the motor fibres. He never found them in purely sensory nerves (as for instance in the periosteum, dura, pulp of the teeth, etc.). They are connected with the large cells of the spinal ganglia and of the nuclei of the sensory cranial nerves. On the basis of these morphological characters and the results of radicotomies recorded in the literature on the subject Professor Kiss considers it probable that these are centrifugal fibres.

The microscopical analysis of the human vagus nerve gave the following results (by osmic acid and by the myelin-method of Weigert):

The intracranial portion of the vagus contains thinly myelinated fibres only, for the greater part, and heavily myelinated fibres (a minority) without any unmyelinated fibres. The picture of a transverse section of the nerve is comparable with that of a posterior spinal root.

The cervical portion of the vagus contains three kinds of fibres. The same thinly and heavily myelinated fibres as in the intracranial portion and in addition a large number of unmyelinated fibres. The author found that the unmyelinated fibres enter the vagus from the superior cervical ganglion of the sympathetic, 6–8 anastomotic branches composed of two kinds of fibres: myelinated and unmyelinated. The structure of these branches agrees with that of the rami communicantes between the sympathetic cord and the spinal nerves. The myelinated bundle corresponds to the white rami (pre-ganglionic and sensory fibres), the unmyelinated to the grey rami (post-ganglionic fibres). The unmyelinated bundles take origin from the cells of the sympathetic ganglion, the thinly myelinated (pre-ganglionic) fibres come from the internal branch of the accessorius (XIth nerve). Vagus and accessorius are in the same relationship to one another as a posterior and an anterior spinal root. The vagus sends 1–2 branches to the accessorius and the accessorius sends 1–2 branches (R. internus) to the vagus. The internal branch of the accessorius contains a great majority of thinly myelinated fibres (pre-ganglionic) and a minority of heavily myelinated (motors for the larynx). Below these anastomoses the vagus is a mixed nerve, like a spinal nerve.

[1] Kiss and Mihalik, "Ueber die Zusammensetzung der periph. Nerven u. den Zusammenhang zw. Morphologie u. Funktion der periph. Nervenfasern." *Ztschr. f. Anat. u. Entwgesch.* vol. LXXXVIII, Nos. 1–2, 1928.

The branches of the mixed vagus contain different kinds of fibres. The external branch of the superior laryngeal nerve, in accordance with its motor function, is composed chiefly of heavily myelinated fibres. The cardiac branches are very different. A cardiac branch of the vagus may be composed mostly of heavily or mostly of thinly myelinated or of even unmyelinated fibres.

The abdominal (subdiaphragmatic) part of the vagus contains a majority (about 75 per cent.) of unmyelinated fibres and a minority (about 25 per cent.) of thinly myelinated fibres. These unmyelinated fibres have their origin not in the vagus, but in the sympathetic. The thinly myelinated fibres may be partially sensory (original vagus), partially pre-ganglionic (sympathetic) fibres for the local ganglionic cells of the stomach. The anastomotic branch of the right vagus to the coeliac ganglion contains fibres exactly similar to those of the abdominal vagus. The connection between the right vagus and the coeliac ganglion is therefore mostly sympathetic like the anastomosis between the phrenic nerve and the coeliac ganglion[1].

The conclusions of the microscopic investigations are as follows:

(1) The vagus originates as an ordinary sensory nerve, its microscopical structure is similar to the posterior spinal roots.

(2) The vagus has the same relationship to the XIth nerve (accessorius) as a posterior spinal root has to the anterior.

(3) The sympathetic has the same relationship to the mixed (motor and sensory) vagus, as it has to an ordinary spinal nerve.

(4) The unmyelinated fibres of the vagus belong to the sympathetic (in Man) and reach the vagus through the anastomotic branches between the vagus and the superior cervical ganglion.

(5) Caudal to these anastomoses a pure vagus is never found.

(6) The cardiac and abdominal branches of the vagus are composed mostly of (sympathetic) fibres which are not originally part of the vagus.

(7) The microscopical analysis of the vagus does not provide any anatomical basis for the existence of a "parasympathetic" system.

In the second part of the demonstration Professor Kiss gave the results of his comparative anatomical studies in Paris made on all classes of Vertebrates (Laboratoire d'Anatomie comparée du Muséum national).

In some Mammals he found the same anastomosis between the right vagus and the coeliac ganglion as in Man.

In other Mammals he found a complete separation in the abdomen between the vagus and the sympathetic. Both vagi terminate on the stomach and the abdominal organs are innervated by the sympathetic branches only.

In birds the two vagi usually unite on the lower third of the oesophagus and the conjoint nerves terminate in the oesophagus. Heart and lungs receive their nerves from the single or from the united vagus. The stomach and all abdominal organs are innervated exclusively by the branches of the sympathetic. The coeliac ganglia are in connection with the sympathetic nerves only.

In Reptiles and in Amphibians the vagi and the sympathetic branches are also completely separated in the abdomen as in birds. Professor Kiss did not find any prevertebral ganglia in many members of these classes.

In Fishes also the two systems are completely separated. The coeliac gang-

[1] Kiss and Ballon, "Contribution to the nerve supply of the diaphragm," *Anatom. Record*, vol. XLI, No. 3, 1929.

lion is an ordinary member of the sympathetic trunk. The sympathetic crosses the cranial nerves in the same topographical relationship to them as to the spinal nerves.

Conclusions (II):

(1) The vagus is a simple cranial nerve which provides the sensory innervation for the superior part of the embryonal digestive tube and the heart.

(2) The effective (motor and secretory) nerve of the abdominal organs is exclusively sympathetic.

(3) The coeliac and all other prevertebral ganglia belong exclusively to the sympathetic.

(4) The so-called parasympathetic influence of the vagus has no anatomical basis in the case of the abdomen. The parasympathetic phenomenon can be only a negative phase of the sympathetic[1].

[1] F. Kiss, "Le rapport entre le pneumogastrique et le grand sympathique." (Communication Préliminaire.) *Archives d'Anatomie, d'Histologie et d'Embryologie*, 1931, t. XIII, p. 163. Definitive article in *Archives du Muséum national d'Histoire naturelle* (1931), Paris.

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